A BIOACOUSTIC ANALYSIS OF RED CROSSBILL (*LOXIA CURVIROSTRA*) VOCALIZATIONS FROM THE ISLAND OF NEWFOUNDLAND, CANADA

by

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A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of Master of Science

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May 2013

ABSTRACT

On the basis of morphological, ecological, genetic and vocal differences, North America Red Crossbills (*Loxia curvirostra*) have been described as a cryptic sibling species complex consisting of at least 10 forms. These forms are most easily differentiated via spectrographic analysis of their vocalizations and are hence known as "vocal types." However, little quantitative work has been done on forms' repertoires. For example, it is unclear if vocalizations, such as those named "excitement calls" or "chitter" by others, vary acoustically depending on the social context in which they are used or the physical state of the caller; it is also not known if such calls have characteristics that are systematically informative. Further, little is known about the vocal behaviour of Red Crossbills on the island of Newfoundland, an island which is generally presumed to contain the endangered Red Crossbill subspecies, *L. c. percna*. I made field recordings (~1000 minutes) of Red Crossbills at 10 sites on the island in order to describe and document structural and contextual variation in vocalizations and to determine categories of calls (Call Classes) that might contain systematic information useful for subsequent comparative analyses. Subjectively classified calls, made on the basis of the social, behavioural, and physical contexts of calling birds, audible qualities of calls, and general appearance of spectrograms, corresponded closely to those of crossbills (*Loxia* spp.) described elsewhere in North America and Europe. In total, adults uttered five Call Classes (I–III, V and VI); juveniles uttered two (IV and V). Both adult males and juveniles of unknown sex also sang. Multivariate clustering of calls, based on the individual averages of 10 acoustic variables measured from 1186 calls, corresponded with the subjectively established Call Classes. Acoustic variability within individuals and

across contexts was relatively low among Call Classes I and III. Call Class II was the most individualistic. A discriminant analysis (DA) on acoustic variables of Class I calls from Newfoundland individuals (n = 83) and individuals of vocal types from elsewhere in North America and Europe (n = 31) classified 89% of birds to the correct vocal type; 98% of birds from Newfoundland were differentiated successfully by DA. Further, many birds from Newfoundland also emitted Class III calls and song motifs that were distinct. Visual examination of Class I spectrograms, including those individuals misclassified by DA, confirmed that seven individuals from Newfoundland were spectrographically and audibly more similar to vocal types 2 and 10, which have been described previously on mainland North America. Thus, the results of this study show that multiple Red Crossbill forms, including possibly *L. c. percna*, are present on the island of Newfoundland.

ACKNOWLEDGMENTS

First, I thank my supervisor, Dr. Ted Miller. Thanks Ted, for all your efforts, many of which went beyond the call. It was a pleasure to work with and be mentored by you.

I also must extend my thanks to Lester Rees and his family for opening up their home to me. Lester has been observing Red Crossbills at his bird feeders since 2005, and has taken a keen interest in Red Crossbill biology. Thanks for sharing your knowledge Lester. I also thank those who generously allowed me to occupy their yards while I recorded crossbills. Those people include Catherine Barrett, Ben and Diane Burton, Loretta Crisby-Whittle, Pauline Drover, and Ashley Tock.

I thank John Gosse, Dr. Luise Hermanutz, and Kirby Tulk for showing confidence in me by agreeing that I was a suitable candidate for this project. I also thank Kirby Tulk and staff at Terra Nova National Park for generously coordinating project funding and providing housing and recording equipment.

Thanks go out to those who took the time to forward Red Crossbill sightings to me. Those people include Kevin Bulter, Rob Cashin, Rod Cox, Ken Knowles, Tina Leonard, Bruce Mactavish, Bruce Rodrigues, John Wells, and Darroch Whittaker. Thanks are also due to Bruce Rodrigues, Greg Stroud, and Dave Fifield, for providing original Red Crossbill recordings. I thank the folks at The Macaulay Library for providing access to their digital archives and Matt Young at Cornell Lab of Ornithology for providing metadata for the Library's crossbill recordings. I also thank Carla Cicero and Rauri Bowie at the Museum of Vertebrate Zoology at UC, Berkeley, for providing access to Jeff Groth's recordings. I also wish to thank Peter Thomas at the Canadian Wildlife Service,

who generously provided recording equipment, crossbill sightings data, and ideas at committee meetings.

I thank the supervisory committee — Dave Innes, Ian Jones, and Bill Montevecchi — for their ideas and encouragement.

Finally, I must thank my family for their unwavering support over the course of the project.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 Introduction

Red Crossbills (*Loxia curvirostra*) are sparrow-sized finches (Fringillidae) that inhabit Holarctic coniferous forests (Cramp and Perrins 1994). They are seed-eating specialists that use muscular hinged jaws, large clasping feet, and curved mandibles that cross at the tip to wrest seeds out of partially closed or closed conifer cones (Newton 1972). Red Crossbill ecology and behaviour are adapted to this specialist diet. For example, populations are irruptive in size and irregular in movements and large numbers of individuals arrive at cone-rich areas and depart cone-depleted areas en masse. Recoveries of individual crossbills in Europe suggest that they may breed in forests separated by up to 4000 km (Newton 2006). Crossbills also exhibit erratic breeding schedules, a trait driven by fluctuating seed availability (Bailey et al. 1953, Tordoff and Dawson 1965, Benkman 1990).

The Red Crossbill has traditionally been considered as a single polytypic species but recent work suggests that it is a complex of cryptic species in both Old and New Worlds. Ten Red Crossbill forms ("pseudospecies"; Knox 1992) may be present in North America and up to 20 may exist elsewhere (Groth 1993, Cramp and Perrins 1994, Benkman et al. 2009, Irwin 2010). The different forms have similar habitats and are difficult to distinguish based on size and plumage, but fine-scaled ecological, behavioural, and genetic differences have been documented. These sympatric ecological forms seem to have arisen due to divergence in foraging traits through utilization of cones from different conifer species (Groth 1988, 1990, Piertney et al. 2001, Parchman et al. 2006, Smith and Benkman 2007, Edelaar et al. 2012). Recent empirical and theoretical work suggests that

ecologically different forms of finches can evolve and persist despite a lack of strict geographic isolation (de León et al. 2010). A possible mechanism that may facilitate divergence with gene flow is through sexual selection of condition-dependent traits, where mate condition reflects the level of ecological adaptation (Snowberg and Benkman 2009, Edelaar et al. 2012). In this scenario, acoustic cues may facilitate discrimination among ecological forms and hence serve as a behavioural mechanism for assortative mating (Podos 2010). While ecological divergence in Red Crossbills appears to be somewhat unique among nomadic bird species, Mallet (2008) suggests that sympatric speciation may be more frequent than thought. Work by Haiman (2011) suggests that such processes underlie the observed morphological and vocal differentiation of highly mobile Evening Grosbeak (*Coccothraustes vespertinus*) populations.

The status of Red Crossbills on the island of Newfoundland. Based on a series of 11 specimens collected in southwestern Newfoundland, Bent (1912) described a new subspecies of Red Crossbill, *L. curvirostra percna*. He noted differences in body size and massiveness of the bill from other North American subspecies recognized at the time, and remarked especially on the much darker plumage colours of *percna* (Bent 1912). Other workers have supported the distinctiveness of *L. c. percna* and it has been generally assumed that its distribution is restricted to the island of Newfoundland (Griscom 1937, Burleigh and Peters 1948, Payne 1987, COSEWIC 2004; but see Bent 1920, Dickerman 1987).

Red Crossbills were considered to be common through the first three quarters of the 20th century (Peters and Burleigh 1951, Erskine 1977) on the island of Newfoundland. Christmas Bird Count data suggest that Red Crossbill numbers on the

island have been declining over the past ~30 years, possibly due to habitat reduction (COSEWIC 2004). At present, *L. c. percna* is listed as Endangered in both Provincial and Federal legislation. However, the identity of Red Crossbills in Newfoundland at present is unclear: is *L. c. percna* still extant? Are other forms of Red Crossbill present? Similar uncertainties about Red Crossbill taxonomy and distribution apply elsewhere. For example, three morphologically similar species are sympatric in Great Britain (Summers et al. 2002).

The use of bioacoustics in taxonomic studies. Acoustic signals of birds function in many important life-history events including predator detection, mate selection, and territorial defence. Sexually selected sounds often diverge rapidly during the process of speciation so are valuable for inferring phylogenetic relationships (Coyne and Orr 2004). The use of acoustic signals in taxonomic studies is now widespread; e.g., sounds have been used to reveal or discriminate among closely related taxa and populations in whales and dolphins (Petrella et al. 2011, Filatova et al. 2012), rodents (Gannon and Lawlor 1989, Matrosova et al. 2012), tree shrews (Esser et al. 2008), primates (Wich et al. 2008), bats (Knörnschild et al. 2010), insects (Fitzpatrick and Gray 2001), frogs (Goicoechea et al. 2010), and birds (Miller 1996). Acoustic signals are also used to detect or identify rare or cryptic species (Lanyon 1969, Johnson 1980, Adkisson 1981, Groth 1990, Whitney 1994, Bierregaard et al. 1997, Henry et al. 1999, Baptista and Krebs 2000, Zimmer et al. 2001, Braune et al. 2008), and are increasingly applied to wildlife monitoring (Delport et al. 2002, Tripp 2004, Fernández-Juricic et al. 2009).

Acoustic analysis of Red Crossbill vocalizations. The subspecies is a formal taxonomic rank that is applied to phenotypically different sets of populations from

different parts of a species' range (Mayr and Ashlock 1991). The subspecies is not a biologically unitary concept (Fitzpatrick 2010) but can be especially useful in reference to geographically discrete breeding populations such as island populations (Cicero et al. 2006). The application of subspecies names to nomadic species like Red Crossbills is problematic, and identification even of well-marked forms is difficult because of irruptions in numbers and space. For example, adults collected during spring and summer may originate from distant areas, and demarcation of distinct populations based on geographic or temporal factors — as often used in other species — is complicated because of temporal and spatial overlap among breeding populations. However, certain calls are reliable markers of different Red Crossbill forms (cryptic species; Groth 1990). Groth (1990) identified seven vocal types of Red Crossbill in continental North America and proposed an eighth for Newfoundland, based on morphological data from museum specimens and a sound recording from a single individual (Pitocchelli 1981). Recent research in Europe has also revealed the existence of distinct vocal types within the *L. curvirostra* complex (Robb 2000).

Calls may not be useful for distinguishing between different Red Crossbill forms if calls change throughout a lifetime (Summers and Piertney 2003), but Sewall (2009) suggested that call learning in adult Red Crossbills is limited, and that use of single vocal types may promote social isolation and hence diversification across different resource-adapted populations. Research on vocalizations of Red Crossbills from the island of Newfoundland could therefore provide information about whether a vocally distinct form is present on the island.

Study objectives. The major goals of my research were to: (1) describe and classify vocalizations of Red Crossbills on the island of Newfoundland; and (2) compare my findings with vocalizations of Red Crossbills from elsewhere in North America. I describe, quantify, and classify calls and songs (Chapter 2), and then analyze vocal variation across micro- and macrogeographic scales (within the island of Newfoundland; between the island and the mainland) and individual birds (Chapter 3). The study provides baseline analyses that will be valuable for future research in unsampled areas (e.g., Canadian Maritimes, St. Pierre and Miquelon, and Cape Breton Island).

Based on knowledge of Red Crossbill vocal differentiation in continental North America and Europe, I predicted that vocalizations recorded from on the island of Newfoundland would differ from mainland populations and would be uniform throughout the island if *L. c. percna* and only *L. c. percna* is present. If *L. c. percna* was not present in samples, I predicted that vocalizations would resemble those described for mainland forms. Finally, if both *L. c. percna* and other forms were present, I predicted a mixture of vocalizations, some like those known for mainland forms and others distinctive and previously undescribed: the latter could be from *L. c. percna*.

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CHAPTER 2. A DESCRIPTION OF RED CROSSBILL (*LOXIA CURVIROSTRA*) VOCALIZATIONS FROM THE ISLAND OF NEWFOUNDLAND, CANADA

2.1 Introduction

Acoustic signals can provide insight into systematics and animal behaviour because they convey information about who is signalling and why (Payne 1986, Bradbury and Vehrencamp 2011). They function in many important life-history events including predator detection, mate selection, and territory defence, and have been used to reveal or discriminate among closely related taxa and populations (Catchpole and Slater 2008, Price 2008). However, before research is conducted on how vocal displays may relate to such things as semantics or taxonomy, an important first step includes characterizing and quantifying the subject's inventory of acoustic signals, i.e., the repertoire (Marler 2004, Boisseau 2005). Such a task can be challenging however: sounds must be recorded from the subject at all ages and seasons and difficult decisions with respect to where categories of sounds begin and end must be made (Marler 2004). Studies that investigate whether acoustic signals differ depending on the physical state or social context of the caller may lead to a deeper understanding of vocal repertoires (Van Horik et al. 2007, Chabout et al. 2012, Henderson et al. 2012). For example, acoustic signals that are found to be relatively unchanging in structure across contexts may encode information about species identity (Marler 1957, Groth 1990), and may be useful in comparative studies.

Vocalizations of the Red Crossbill (*Loxia curvirostra*), a cone-obligate, seed-eating specialist of Holarctic forests, may play an important role in delineating different vocal forms ("types"; Groth 1993a). During extensive studies of Red Crossbills in North

America, Groth (1984, 1988, 1990) subjectively classified their calls into several distinct categories; vocalizations from a well-documented form of Red Crossbill he called "type 2" (a form possibly representative of *L. c. pusilla*) were categorized into 17 classes (referred to herein as Call Classes). Red Crossbill song also was assigned to its own category but was not analysed in detail (Groth 1990). Groth (1990) suggested that at least three of the Call Classes, namely, "flight", "excitement", and "alarm", encoded species-specific information because they were tied to morphologically and ecologically different forms. On this basis, Groth (1990) recognized a total of eight vocal types for North America. Recently, Robb (2000), Summers et al. (2002), Benkman et al. (2009), and Irwin (2010) have used some of the same Call Classes to help delimit previously undescribed Red Crossbill forms from elsewhere in North America and Europe.

Despite much recent research activity, important gaps in knowledge of the vocal behaviour of Red Crossbills exist, for example: descriptions of vocalizations are lacking from many parts of the range (e.g., eastern Canada); few quantitative analyses are available; and vocal variation in Call Classes across individual birds is essentially unknown. It is also not known to what extent song or other Call Classes (e.g., "chitter"; Groth 1990) encode diagnostic information about vocal forms, or if these forms utilize all of the type 2 Call Classes described by Groth (1990).

Sound analysis and recording techniques have also improved greatly since Groth's (1990) seminal descriptions. Many sound analysis programs facilitates accurate and repeatable measurement of animal sounds (Zollinger et al. 2012, Ou et al. 2013). For example, spectral values can be extracted from sounds using frequency tracking algorithms (e.g., Boersma 1993), making it possible for acoustic data to be extracted from

frequency contours. Such tools offer repeatable and unbiased ways to measure vocalizations over more traditional methods of data collection, i.e., "eyeballing" spectrograms, where rough spectrographic measurements are made visually with screen cursors on spectrograms (Zollinger et al. 2012).

I investigated vocalizations of Red Crossbills on the island of Newfoundland, Canada. The island is generally thought to have an endemic subspecies of Red Crossbill, *L. c. percna* (Griscom 1937, Burleigh and Peters 1948, Payne 1987, COSEWIC 2004). Groth (1990) also proposed that the island of Newfoundland contained its own corresponding vocal form, type 8. However, supportive acoustic evidence was weak and based on only a brief sound recording from a single bird (Pitocchelli 1981, Groth 1990). Nonetheless, recent work by Young et al. (2012) suggested that Red Crossbills from the island of Newfoundland uttered at least one Call Class that was distinct from other vocal forms described elsewhere in mainland North America.

The Red Crossbills of Newfoundland offer a unique opportunity to study the vocal behaviour of poorly known Red Crossbill population. Objectives of this chapter are to: (i) quantitatively classify the vocalizations of Red Crossbills from the island of Newfoundland on the basis of new field recordings; (ii) describe the resulting Call Classes on the basis of their acoustic qualities and the contexts (i.e., social, physical) in which they are uttered; and (iii) determine which Call Classes are useful for comparison with samples from elsewhere (Chapter 3).

Terminology of Red Crossbill calls. Despite the relatively small vocal repertoire of Red Crossbills, varied names have been applied to Call Classes. For the most common call in the repertoire, some authors have used onomatopoeic descriptors such as *dyip*, *jip,*

and *chip* (Nethersole-Thompson 1975, Cramp and Perrins 1994, Constantine and The Sound Approach 2006). Sewall (2008) referred to these calls as "contact calls"; others have used the name "flight call" (Groth 1993a). Such names probably vary in part due to acoustic variation within Call Classes and because single Call Classes are used in multiple social contexts (context-dependent communication is especially pronounced in species with small repertoires; Smith 1969, 1977, 1997). For example, Red Crossbills sometimes give "excitement calls" (Groth 1993a) in agonistic contexts with heterospecific birds (e.g., corvids; this study) or in breeding contexts with conspecific birds (e.g., from males before flying to the nest to feed brooding hens; Nethersole-Thompson, 1975). In closing, I avoid the use of such names because they are not descriptive and invariably imply single functions that reflect arbitrary views of different observers. Instead, I employ the use of neutral terms (i.e., Roman numerals; see Table 2.1) for describing calls so that function is not prematurely presumed (Miller 1991, Martin and Bateson 1993).

TABLE 2.1. Summary of Call Classes proposed in this study in relation to other studies involving crossbill (*Loxia* spp.) vocalizations.

Call Class	Contexts of use (this study) and remarks	Synonyms (citation)
I	*Contexts*: Full flight; during feeding behaviour; pivoting; perched *Remarks*: Usually louder than Call Class II; sometimes grades into Call Class II	*chip* (3); contact (10); *dyip*-call (5, 13); flight call (4, 6, 7, 9, 11, 12); travelling call (2)
II	*Contexts*: Perched; short-distance movements within or between trees while foraging; pivoting; descending to ground to drink *Remarks*: Usually soft but sometimes as loud as Call Class I; sometimes grades into Call Class I	chitter (4, 6, 7,12); communication call (2); contact call (8); *wik*, *peep* (3)
III	*Contexts*: In response to heterospecific animals entering foraging space[a] or seen overhead[b]; between interacting crossbills (e.g., males attempting copulation) *Remarks*: Sometimes inserted into song	alarm call (2, 4, 7, 12); excitement call (4,6,7,9,11,12); *toop* (3, 4, 12); *tep* (5, 13); *tuck, tuck, tuck* (1); *tut-tut* (6)
IV	*Contexts*: Given by dependent juveniles[c] as they follow parents near bird feeders or through forests *Remarks*: Very common, distinct	begging or *chitoo* call (4, 5, 6, 7); *sit-seecher/pit-chu chu chu* (5, 13)
V	*Contexts*: aggressive crossbills at feeding sites *Remarks*: Rare, atonal	threat call (7)
VI	*Contexts*: aggressive crossbills at feeding sites (may be directed at heterospecific birds) *Remarks*: Rare, atonal	distress call (4)

[1]Tordoff 1954; [2]Bailey et al. 1958; [3]Nethersole-Thompson 1975; [4]Groth 1990; [5]Cramp and Perrins 1994; [6]Adkisson 1996; [7]Robb 2000; [8]Knox cited by Robb 2000:65; [9]Summers et al. 2002; [10]Sewall 2008; [11]Benkman et al. 2009; [12]Irwin 2010; [13]see Cramp and Perrins (1994) for others.

[a] Observed: dog (*Canis familiaris*), Common Starling (*Sturnus vulgaris*), Blue Jay (*Cyanocitta cristata*), Gray Jay (*Perisoreus canadensis*).

[b] Observed: Osprey (*Pandion haliaetus*); Herring Gull (*Larus argentatus*).

[c] Identified by brownish heavily streaked plumage (Pyle 1997).

2.2 Methods

Study area and sample. Red Crossbills were recorded ad libitum at 10 localities in on the island of Newfoundland between 4 February 2010 and 2 August 2011. Seven sites were in rural or suburban areas: Clarenville and Glovertown in central Newfoundland, and Conception Bay South, Goulds, La Manche, South River, Upper Gullies, and Whitbourne on the Avalon Peninsula in eastern Newfoundland (Fig. 2.1; Table 2.2). Many recordings at these sites were made near bird feeders on private property or in nearby forest. Forest habitat was mainly mature boreal forest, with black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) as the dominant conifer species. White spruce (*Picea glauca*) and American larch (*Larix laricina*) were also common, and crossbills were observed feeding in both. In Clarenville, Glovertown, and Whitbourne, cultivated pine (*Pinus* spp.) was present and crossbills also foraged on them. At the two western sites (West Brook Ecological Reserve and Howley) crossbills were recorded in forests dominated by red pine (*Pinus resinosa*); these forests are the largest natural stands of red pine remaining in Newfoundland (Roberts 1985). Red Crossbills were also seen in white pine (*Pinus strobus*), and adjoining spruce, fir, and larch forests at these sites.

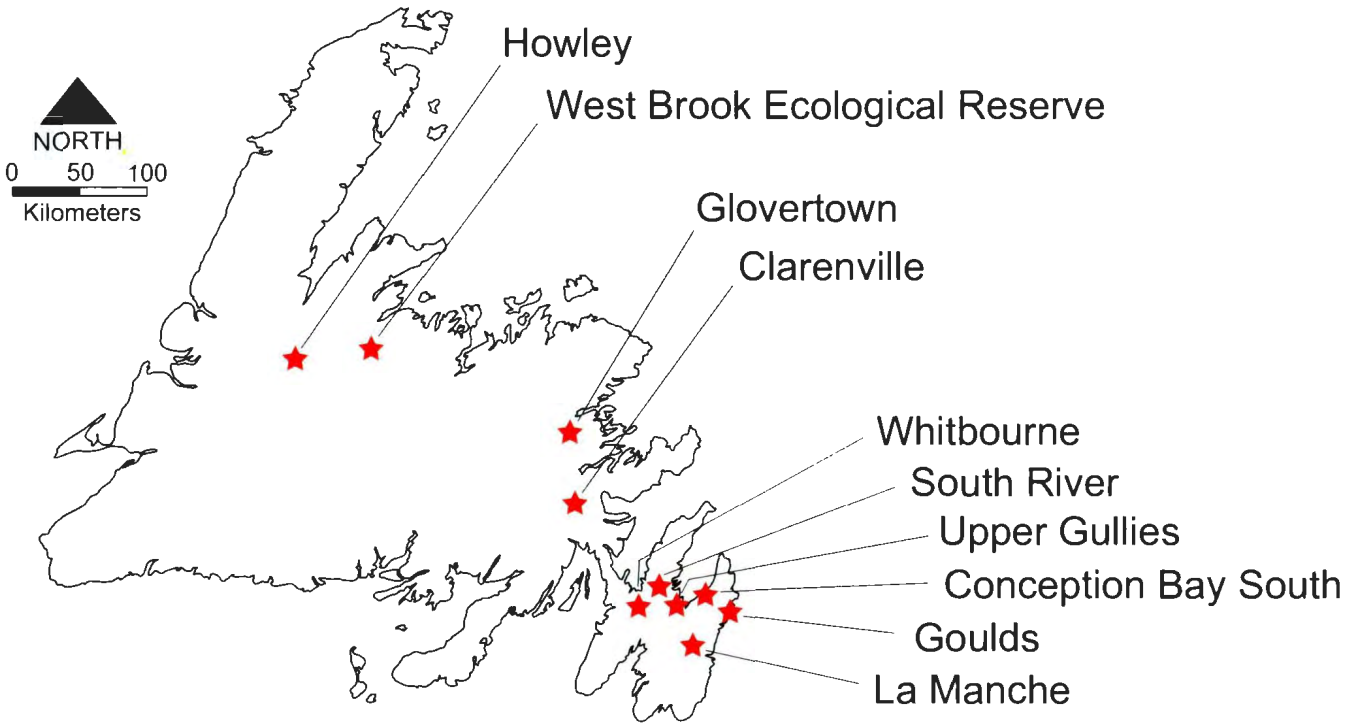

FIGURE 2.1. Sound recordings of Red Crossbill (*Loxia curvirostra*) were made between 4 February 2010 and 2 August 2011 at 10 sites across Newfoundland, Canada, six of which were on the Avalon Peninsula. Stars show the sampling localities; coordinates are given in Table 2.2.

TABLE 2.2. Summary of metadata for Red Crossbills (*Loxia curvirostra*) seen or recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Approximately 130 crossbills were encountered in 10 sites. "No. adults recorded" refers to number of individual adults from which I recorded Class I calls.

Location	No. birds seen[a]	No. adults recorded	Recording Dates
Howley 49°10' N 57°05' W	18 (0)	9	2011: 30 April,1–2 May
West Brook Ecological Reserve 49°15' N 56°20' W	7 (5)	2	2011: 30 June
Glovertown 48°40' N 54°02' W	18 (0)	7	2011: 28–29 January
Clarenville 48°10' N 53°57' W	23 (0)	7	2011: 18 February, 26–27 June
Whitbourne 47°24' N 53°31' W	24 (8)	13	2010: 17 & 22–23 May, 16 July 2011: 9 & 11 March, 13 April, 8 June, 30 July
South River 47°30' N 53°17' W	16 (0)	8	2011: 1, 8 & 10 June
Upper Gullies 47°29' N 53°02' W	14 (0)	9	2011: 21–22 June
Conception Bay South 47°30' N 52°55' W	20 (8)	17	2010: 4 February, 31 March, 28 April 2011: June 11, 17, 21
Goulds 47°27' N, 52°44' W	10 (0)	10	2011: 18 July, 1–2 August
La Manche 47°10' N, 52°55' W	2 (0)	1	2011: 8 July
Totals	130	83	33 recording days

[a] No. adults (no. juveniles); crossbills with brownish heavily streaked plumage were identified as juveniles (Pyle 1997).

During the study, Red Crossbills were recorded on 33 days, producing approximately 1000 minutes of raw recordings. All recordings were made with a Fostex FR–LE2 field recorder, a Telinga Pro Series microphone and a 570 mm Telinga parabola. Calls were sampled at 44.1 Hz and digitized at 16 bits. Continuous recording and observation sessions ranged from a few minutes to as long as 4 hours, depending on the birds' behaviour (e.g., flying overhead, foraging in trees, or feeding at bird feeders or in trees). Most recordings were made at distances of 10 to 30 m from the birds.

I followed individual birds, pairs, and groups for extended periods and dictated oral records of their behaviour into the field recorder. Subsequently, recorded individuals were identified on spectrograms using the recorded field notes; birds were not banded. I reduced the number of possible replicated recordings from the same individual by recording at sites that where relatively well separated and by not considering individuals of groups with the same number of similarly plumaged males/females/juveniles encountered on the same day or contiguous days as different individuals. To determine whether call structure varied with behaviour, I noted in particular whether birds were flying or perched while vocalizing (certain Call Classes were uttered in multiple contexts). Perched birds were defined as those perched in trees, whether resting, feeding, or vigilant. I judged birds to be flying when in full flight, e.g., when travelling out of the immediate recording area. Sex and relative age of the birds were determined by plumage characteristics: dark, heavily streaked individuals were assumed to be juveniles (Pyle 1997) and unstreaked birds were considered to be adults. Birds that were bright yellow, orange, or red were identified as males; light yellow, greenish, or grayish-olive birds were identified as females (Phillips 1977; Groth 1993a).

Characterization of calls. I selected only recordings of high quality for multivariate analysis; recordings with much background noise or with overlapping vocalizations of multiple individuals were excluded. To standardize sound files, individual calls were copied from the original recordings and saved to separate WAV files. These calls were then band-pass filtered (lower limit = 750 to 1,000 Hz; upper limit = 6000–6500 Hz) using Raven Pro 1.4 (Charif et al. 2009). In some cases, background noise was also filtered manually by clicking and dragging around the unwanted signal and using the "Filter Out Active Selection" tool in Raven. The filtered WAV files were transferred to the computer program Praat 5.3.02 (Boersma and Weenink 2011). Here, I extracted frequency contours from the fundamental frequencies (f_0) of calls with Praat's frequency tracker in the "SoundEditor" window. Intensity contours, derived from the call's waveform, were also extracted. The SoundEditor window was set to a frequency view range of 1–6.5 kHz with a vertical range on the intensity axis of 50–100 dB/Hz. The time step (i.e., frequency sample rate) of the frequency contour was 0.0005 s (thus, a 49.5 ms call provided 100 frequency sample points). The "Extract visible pitch contour" and "Extract visible intensity contour" functions of the SoundEditor window allow one to extract the visible frequency and intensity points on the spectrogram, so I enlarged the call with the on-screen cursor so that only it was contained within the SoundEditor window. In this way, I avoided extracting frequency points that were not part of the call under analysis (e.g., points due to echo or extraneous sound sources).

A total of 11 frequency, intensity and temporal, variables were taken from contours of tonal calls (Fig. 2.2; Table 2.3). The start frequency of a call (F1) was defined as the first frequency point of the contour; the end frequency of a call (F2) was

represented by the final frequency point of the contour. The minimal (F3) and maximal frequencies of a call (F4) were taken from the minimal and maximal values along the frequency contour. The frequency at the maximal intensity of the call (F5) was the frequency at the maximal intensity of the intensity contour. The mean frequency of the call (F6) was determined by dividing the sum of the frequency samples from a frequency contour by the total number of samples. The mean absolute slope of a call (F7), a measure of the average local variability in f_0, was determined by: (1) computing the slope between adjacent points on the frequency contour, (2) repeating this calculation for all points, and (3) calculating the subsequent average slope for the whole contour (the differences in slope directions are not considered). For example, if two consecutive points had a difference of 10 Hz, and the time step was 0.0005 s, the local slope was 20 000 Hz/second. Thus, a rise of 10 Hz and a fall of 10 Hz both count as a slope of 20 000 Hz/second. The duration of calls (D1) was computed as the difference between end and start times of the frequency contour. Intensity measures (I1 and I2), like the frequency variables, were computed directly from intensity contours derived in Praat. The 11 variables were extracted from spectrograms using a custom written script. Calls with energy spread across a relatively broad frequency band (i.e., Call Classes IV–VI; Fig. 2.3) were not characterized with frequency contours. Instead, acoustic variables were measured manually with the on-screen cursor. To determine temporal patterning of calls, I measured inter-call intervals (ICIs) on spectrograms. Descriptions of nonlinearities in vocalizations of follow Tyson et al. (2007).

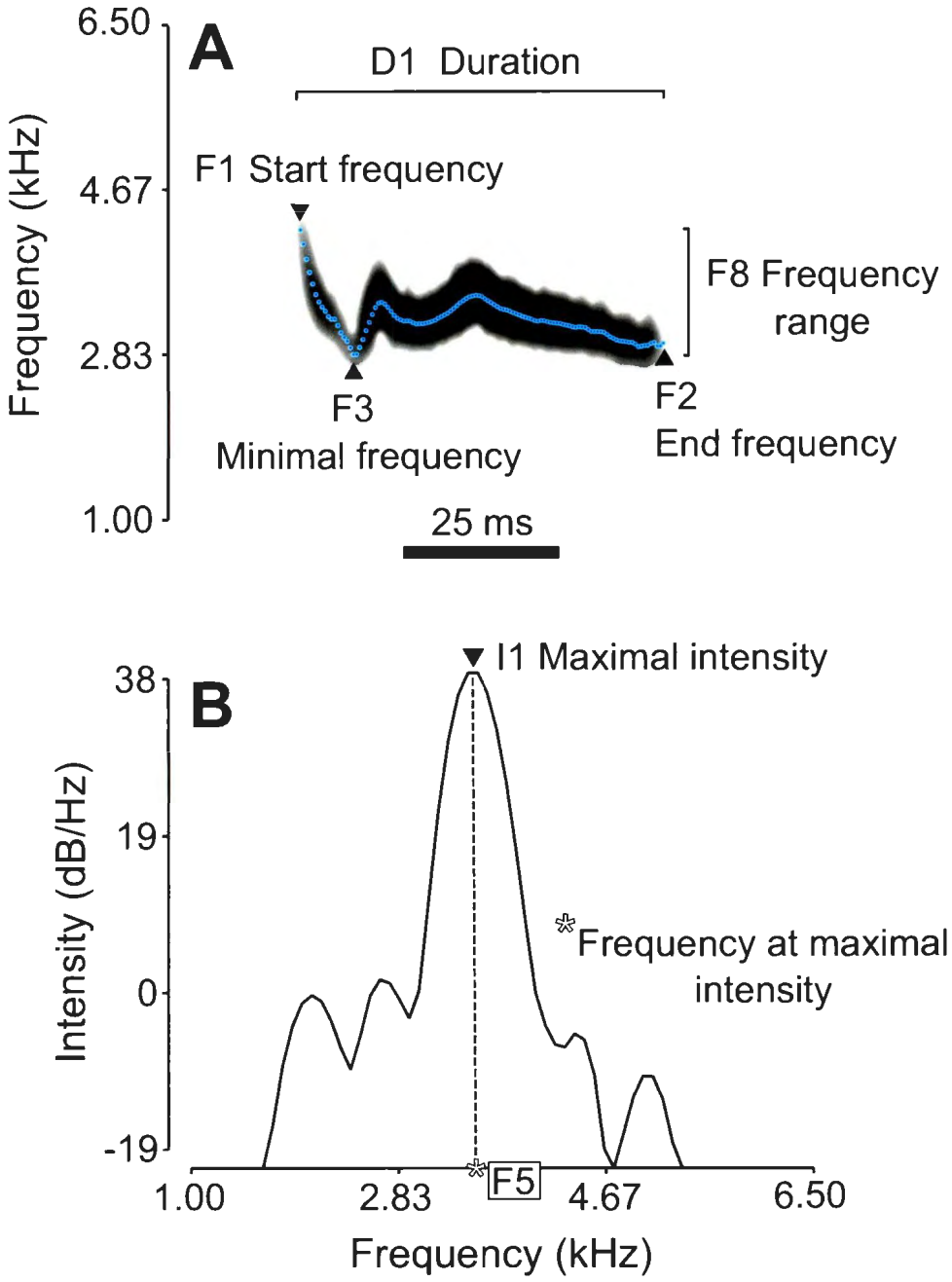

FIGURE 2.2. (A) Acoustic measurements were taken directly from frequency contours (blue points) derived from spectrograms (see Table 2.3 for descriptions of variables) using Praat 5.3.04 (Boersma and Weenink 2011). (B) Graphical illustration of how maximal intensity (I1) and frequency at maximal intensity (F5) were measured via spectral slice analysis.

TABLE 2.3 Summary of acoustic variables measured on Red Crossbill (*Loxia curvirostra*) vocalizations recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. See text for details.

Variable abbreviations	Description
Frequency variables (in Hz except F7):	
F1	Frequency at start
F2	Frequency at end
F3	Minimal frequency
F4	Maximal frequency
F5	Frequency at maximal intensity
F6	Mean frequency
F7 (Hz/s)	Mean absolute slope
F8	Frequency difference between F4 and F5
Temporal variable (ms):	
D1	Duration
Intensity variables (dB/Hz):	
I1	Maximal intensity
I2	Intensity at maximal frequency

Classification and statistical analysis of vocalizations. I first classified Call Classes subjectively on the basis of social, behavioural, and physical contexts of the calling birds, audible qualities of calls, and general appearance of spectrograms. To explore acoustic structure quantitatively and to confirm identification of Call Classes, vocalizations were subjected to several multivariate statistical techniques. These analyses were performed on the individual means of variables to determine which variables contributed most to acoustic variability. Principal components were based on correlation matrices, which are preferred over covariance matrices when variables have different units (ms, Hz, and dB/Hz in this case; Jolliffe 1986, Baayen 2008). One variable (F8) was a derivative of two others (F4, F5) and so was omitted from multivariate analyses.

A discriminant analysis (DA) was performed on the individual means of variables to determine whether individuals could be classified by Call Class. Call Classes were also subjected to hierarchical agglomerative clustering (HAG), an unsupervised multivariate algorithm, to confirm *a priori* classifications of subjectively defined Call Classes. Acoustic variables were scaled by z-transformation prior to cluster analysis, and the Manhattan distance measure was used as it is less affected by outliers in the data set (Gower and Legendre 1986, Warton and Hudson 2004). I used Ward's method as the linkage technique to form clusters.

To investigate acoustic individuality, I computed coefficients of variation (CVs): (a) between individuals ($CV_b = (SD/X_{mean}) \times 100$), where X_{mean} is the overall mean and SD is the standard deviation for each call parameter; and (b) within individuals ($CV_w = (SD/X_{mean})(1.25n) \times 100$), where X_{mean} is the mean, SD is the standard deviation of the individual means, and n is the number of calls per individual (Sokal and Rohlf 1995). The ratio CV_b/ mean CV_w was used as a measure of between-individual variation relative to within-individual variation for each variable (Robisson et al. 1993). To investigate potential differences between acoustic variables measured from birds vocalizing in various social and behavioural contexts, I used univariate nested ANOVAs and Wilcoxon tests.

I used R version 2.14.0 (R Development Core Team 2011) for all analyses and graphics, particularly: ggplot 2 0.8.9 (data visualization; Wickham 2009); RColorBrewer (colours for data visualization; Neuwirth 2011); ggbiplot (PCA visualization; Vu 2011); plyr (data analysis; Wickham 2011); plotrix (plots with two ordinates; Lemon 2006); coin (Wilcoxon tests; Hothorn et al. 2008); MASS (discriminant analysis; Venables and Ripley

2002); ape (variance components; Paradis et al. 2004); and nlme (nested models; Pinheiro et al. 2011).

2.3 Results

Overview of Call Classes. I recognized six Call Classes that were uttered from Red Crossbills. Five Call Classes were uttered from adults (Classes I–III, V and VI); two were uttered by juveniles (Classes IV and V; Fig. 2.3). Both adults and juveniles were also recorded singing. Call Classes I, II and III were brief frequency modulated tones with the dominant frequency between ~1–6 kHz. When harmonics (frequency of the signal that is an integer multiple of the fundamental frequency) were present, they were relatively weak in Classes I and II and strong in III and IV (Fig. 2.3). Some calls within Classes I and IV exhibited non-linear phenomena such as biphonation (defined here as two independent frequencies being produced simultaneously; Tyson et al. 2007). Call Class IV was the most complex Class, with sounds that often combined non-linear phenomena such as biphonation, subharmonics (spectral components which appear as fractional integer values of an identifiable f_0), or deterministic chaos (with energy across a broad frequency band; Tyson et al. 2007). Call Classes V and VI always exhibited deterministic chaos.

Calls in Classes I–III often were uttered as series. To determine whether the temporal pattern of vocalization differed across Classes, I measured 556 ICIs from 36 individuals. ICIs were centered on one peak for each Call Class: 150 ms for I, between 100–125 ms for II and 175 ms for III (Fig. 2.4).

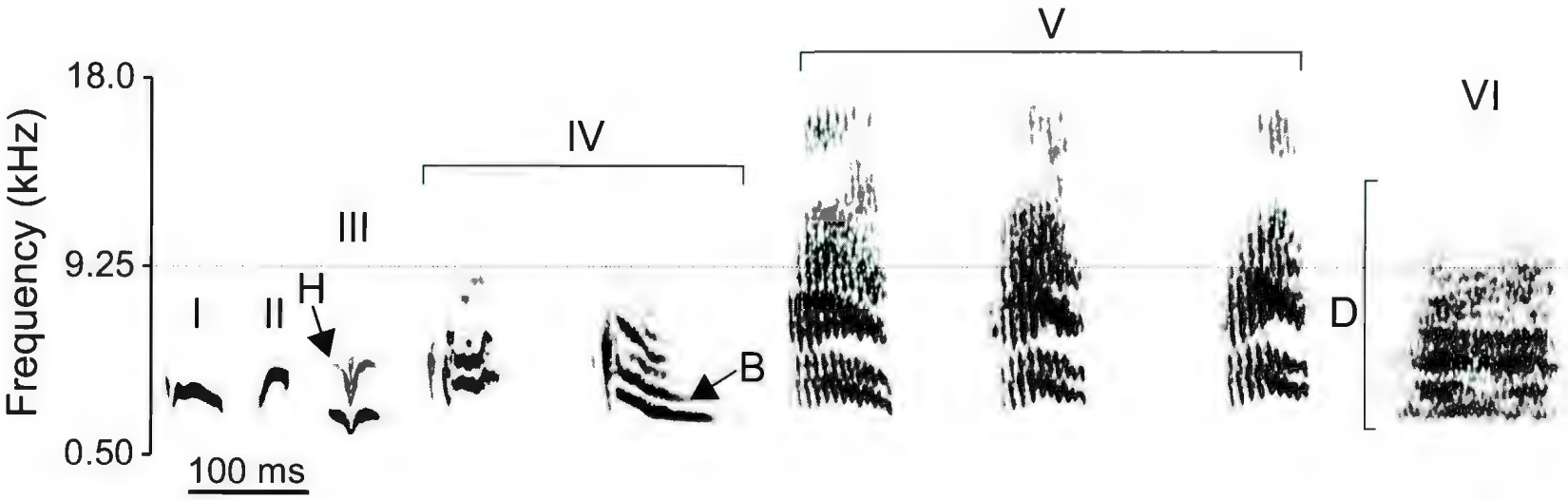

FIGURE 2.3. (I-VI) Examples of Call Classes of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Call Classes I–III were frequency modulated tones. Of these three, Call Class III typically produced the strongest harmonics (H). Call Classes IV, V, and VI were harsher and more complex, and commonly exhibited non-linear phenomena such as biphonation (B) and deterministic chaos (D).

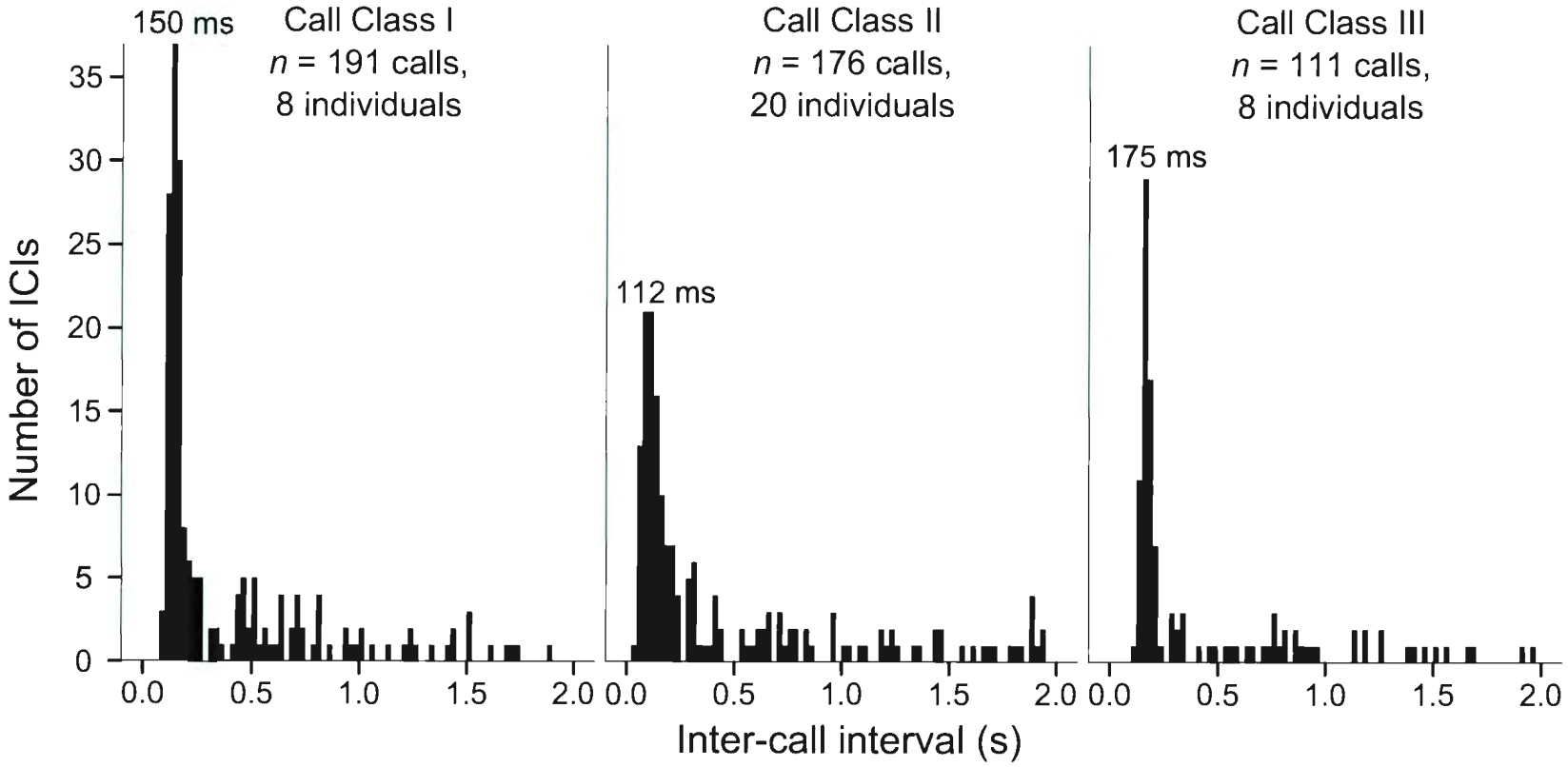

FIGURE 2.4. Distribution of ICIs (inter-call intervals) up to 2 s (n = 478) for Call Classes I–III of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. A further 78 intervals, ranging from 2–87 s (mostly from Call Class II), are not represented along the x-axis but showed no peaks in distribution. The numbered peaks represent approximate modes.

Multivariate classification of Call Classes. Acoustic variables were extracted from 1211 calls from 131 individuals across Call Classes I–VI (Table 2.4). A PCA on the individual averages of 10 acoustic variables from Calls Classes I–III (1186 adult calls from 125 individuals) corresponded with the Call Classes that were established subjectively (Table 2.5; Fig. 2.5). The first two PCs accounted for about two-thirds of the original variation among the variables; the first PC alone explained almost half of the total variance and was correlated with relatively high-frequency calls. Variables F4 (maximal frequency of call), F5 (frequency at maximal intensity of call), and F6 (mean frequency of call) segregated into a distinct group of correlated variables (Fig. 2.5). These three variables produced relatively high loadings (salient variables are those with loadings >0.40; Guadagnoli and Velicer 1988) and were important in distinguishing Call Classes I and II from Call Class III along the first PC. The second PC explained almost one-fifth of the variance; salient variables along this component were I1 (maximal intensity of call) and D1 (duration of call). Here, Call Classes II and III were distinguished from the louder and longer calls of Class I. Figure 2.5 also depicts overlap between Class I and II calls; these Call Classes are known to intergrade to some degree (Groth 1990, Robb 2000, Irwin 2010), and I recorded some calling sequences in which Class I and Class II calls intergraded. Call Class III was discrete and did not intergrade with the other Call Classes.

TABLE 2.4. Descriptive statistics (grand mean ± SD, range in parenthesis) for variables (*n* calls = 1211) on six Call Classes of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011.

	Call Class (*n* individuals, calls):					
Acoustic variable[a]	I (83, 890)	II (30, 174)	III (12, 122)	IV (3, 17)	V (2, 7)	VI (1, 1)
Frequency variables (in Hz except F7):						
F1	3897 ± 493 (2930–5159)	3458 ± 420 (2665–4388)	2407 ± 260 (1696–2687)	—	—	—
F2	3113 ± 541 (1958–5220)	4088 ± 797 (2740–5838)	2306 ± 104 (2180–2465)	—	—	—
F3	2868 ± 243 (1958–3365)	3227 ± 336 (2665–4177)	1878 ± 227 (1435–2156)	1856 ± 548 (1219–3086)	2677 ± 701 (1787–3604)	1750
F4	4300 ± 365 (3540–5220)	4590 ± 517 (3661–5844)	2572 ± 171 (2271–2907)	13906 ± 1595 (11810–17270)	17230 ± 5586 (11100–2690)	19570
F5	3633 ± 182 (2955–4138)	4020 ± 486 (3366–5425)	2375 ± 129 (2094–2554)	—	—	—
F6	3534 ± 176 (2885–4058)	3903 ± 405 (3391 5202)	2303 ± 112 (2054–2452)	—	—	—
F7 (Hz/s)	73317 ± 24793 (28284–177902)	92703 ± 32282 (34489–180976)	42742 ± 15543 (23807–17977)	—	—	—
F8	1433 ± 409 (600–2507)	1363 ± 562 (511–3179)	694 ± 228 (324–1046)	12051 ± 1244 (9844–14931)	14553 ± 6250 (7496–20254)	17820
Temporal variable (ms):						
D1	50 ± 6 (34–63)	27 ± 6 (15–41)	48 ± 4 (43–53)	107 ± 23 (68–144)	74 ± 13 (56–90)	137
Intensity variables (dB/Hz):						
I1	75 ± 5 (58–86)	68 ± 6 (52–77)	71 ± 7 (59–80)	74 ± 3 (68–78)	72 ± 6 (66–79)	73
I2	60 ± 9 (36–78)	61 ± 9 (42–76)	60 ± 7 (48–70)	—	—	—

[a]F1: Frequency at start; F2: Frequency at end; F3: Minimal frequency; F4: Maximal frequency; F5: Frequency at maximal intensity; F6: Mean frequency; F7: Mean absolute slope; F8: Frequency difference between F4 and F5; D1: Duration; I1: Maximal intensity; I2: Intensity at maximal frequency; Descriptions of variables are in Table 2.3.

TABLE 2.5. Summary of results of principal components analysis based on measurements on Call Classes I–III (1186 calls from 125 individuals) of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011.

	Variable loadings (Percent of explained variance)		
Acoustic variable[a]	PC1 (48%)	PC2 (19%)	PC3 (14%)
F6	–0.44	0.09	0.09
F4	–0.42	0.12	–0.09
F5	–0.42	0.12	0.14
F3	–0.38	0.09	0.05
F2	–0.35	–0.26	0.03
F7	–0.28	–0.07	0.05
F1	–0.26	0.37	–0.48
D1	0.20	0.48	–0.41
I2	0.07	0.32	0.72
I1	0.06	0.64	0.20

[a]F1: Frequency at start; F2: Frequency at end; F3: Minimal frequency; F4: Maximal frequency; F5: Frequency at maximal intensity; F6: Mean frequency; F7: Mean absolute slope; D1: Duration; I1: Maximal intensity; I2: Intensity at maximal frequency; Descriptions of variables are in Table 2.3.

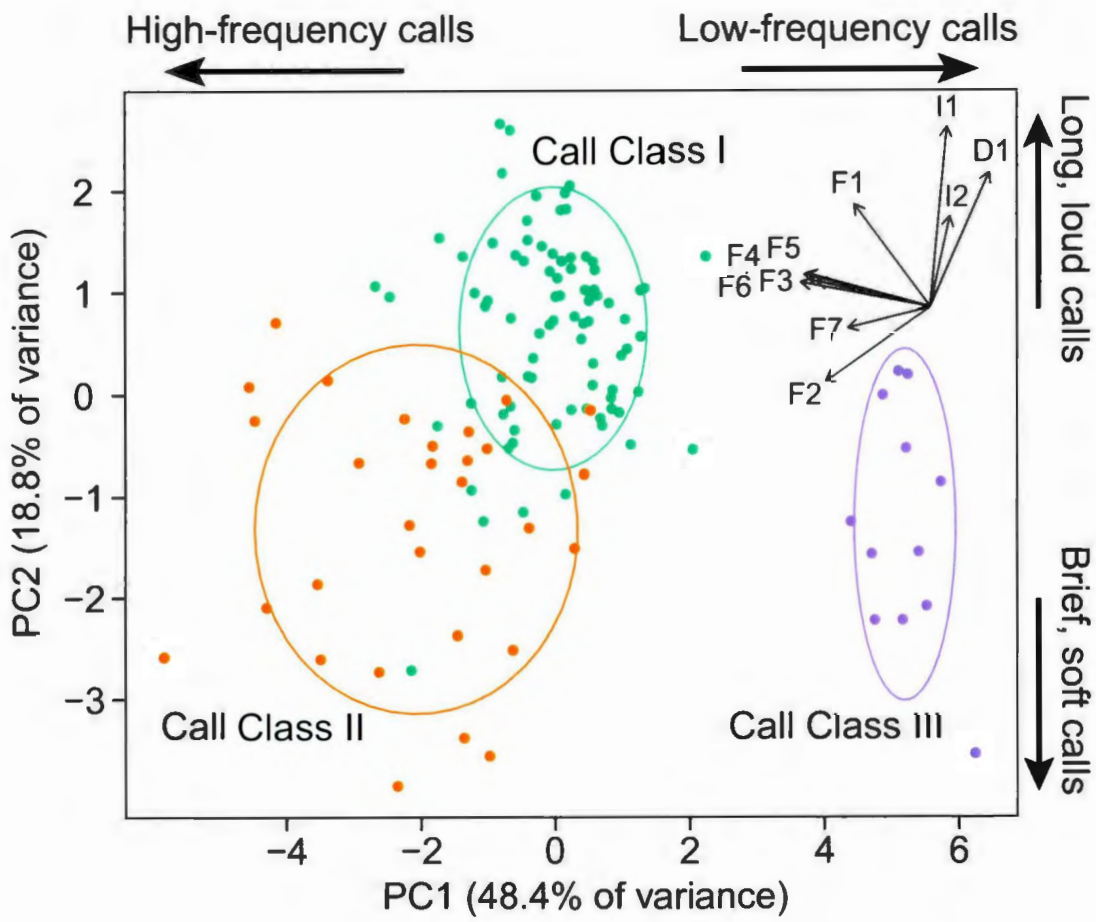

FIGURE 2.5. Principal components analysis (PCA) on Red Crossbill (*Loxia curvirostra*) vocalizations (1186 calls from 125 individuals) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Three Call Classes are suggested. Loadings were highest on mean frequency (F6) and maximal intensity (I1) for principal components 1 and 2, respectively. Ellipses are ± 1 SD data ellipses, Call Classes are shown by different colours. The ray diagram (top right) summarizes variable loadings. Abbreviations are F1 (start frequency), F2 (end frequency), F3 (minimal frequency), F4 (maximal frequency), F5 (frequency at maximum intensity), F6 (see above), F7 (absolute mean frequency), D1 (call duration), I1 (see above), and I2 (intensity at maximal frequency).

Hierarchical cluster analysis on individuals confirmed my subjective classifications: 93.6% of individuals grouped into the same Call Classes (Fig. 2.6). Eight of 125 individuals did not group into Call Classes that were recognized *a priori*. Five of these individuals (nos. 7, 9, 19, 56, and 58; see Fig. 2.6) were originally identified as Call Class I individuals but clustered into Call Class II. The other three individuals (nos. 59, 102, and 105), conversely, were grouped into Call Class I but had been classified subjectively as Call Class II. These latter individuals produced acoustic variables with values near the upper and lower extremes of their range or, in some cases, were outliers (i.e., samples greater or less than 1.5 times the inter-quartile range; Tukey 1977).

Discriminant analysis classified 98% (123/125) of individuals to subjectively recognized Call Classes (Fig. 2.7). Again, only individuals from Call Classes I and II were misclassified (one Call Class I individual was classified as Call Class II and vice versa). These individuals had mean contour durations that were at the extremes of their respective domains (38.4 ms for Call Class I; 40.9 ms for Call Class II).

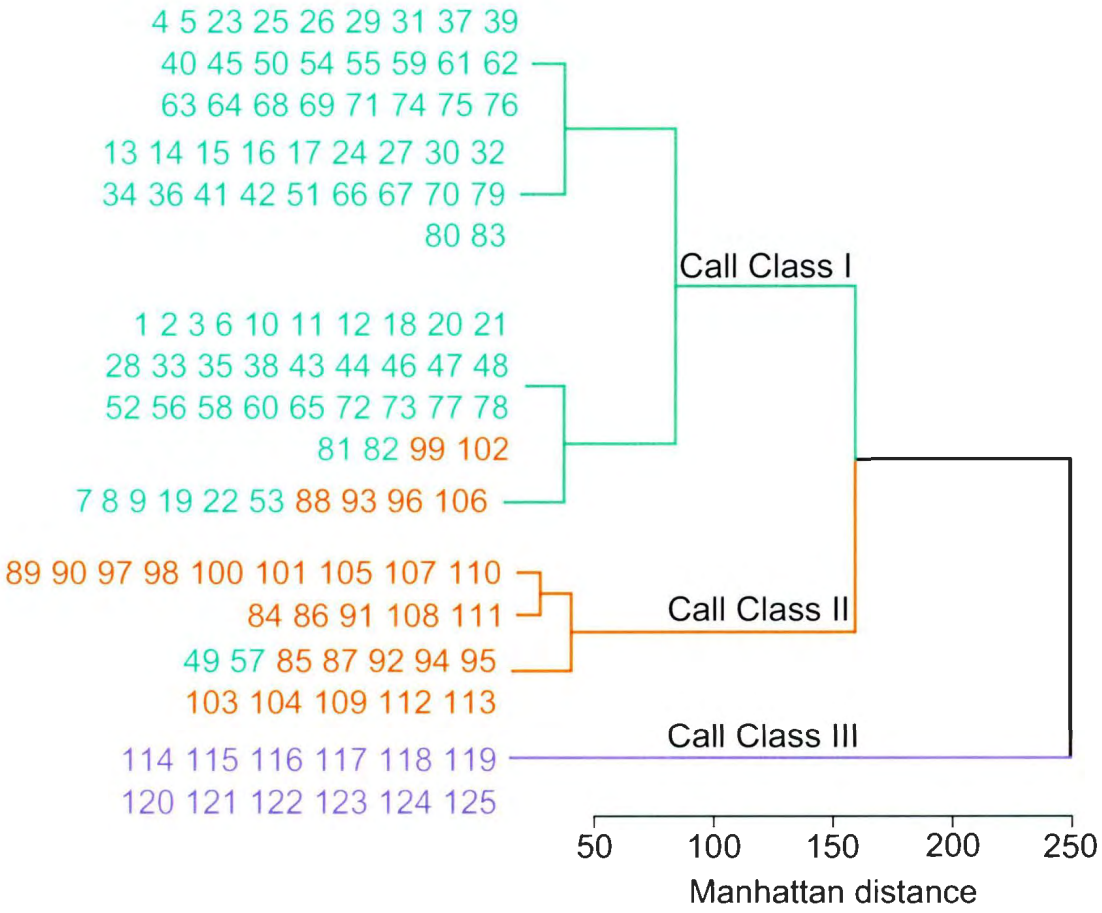

FIGURE 2.6. Dendrogram illustrating results of the cluster analysis on individual averages of call variables (Call Classes I, II, and III; *n* calls = 1186) recorded from 125 Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Calls from eight individuals (nos. 49, 57, 88, 93, 96, 99, 102, and 106) did not match the subjectively established Call Classes (shown by different colours).

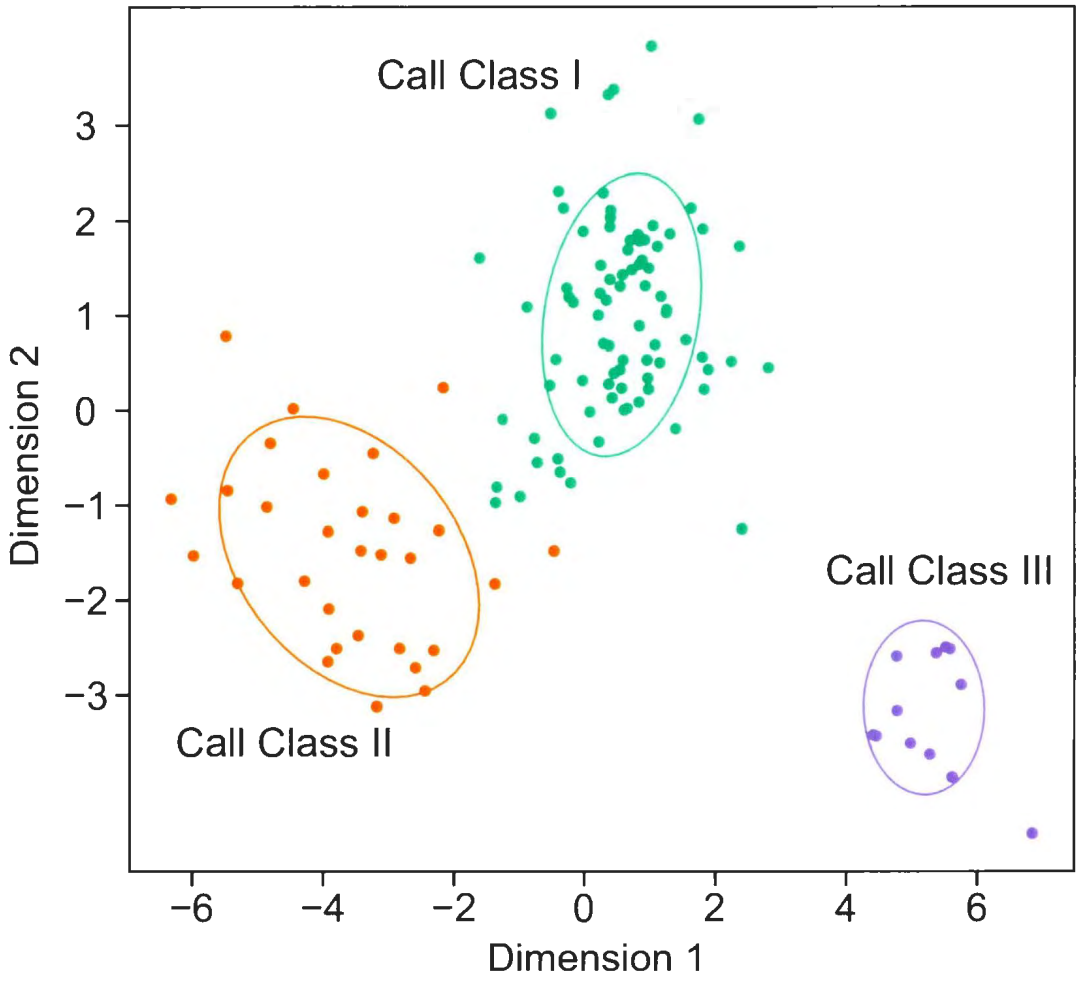

FIGURE 2.7. Discriminant analysis on the individual averages of 1186 calls from 125 Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. The analysis classified 98% of individuals to subjectively established Call Classes. The two misclassified individuals (one Call Class I as a Call Class II and vice versa) uttered vocalizations of intermediate duration between Call Classes I and II. Ellipses are 95% confidence intervals; Call Classes are shown by different colours.

Most acoustic variables from Call Class II were more variable among than within individuals (i.e., CV_b/mean CV_w ratios > 1.0), suggesting that these variables may encode information about individual identity. In contrast, little individuality was expressed in Call Class III variables: CVs were consistently higher within than among individuals (Fig. 2.8). Calls from Class I were intermediate.

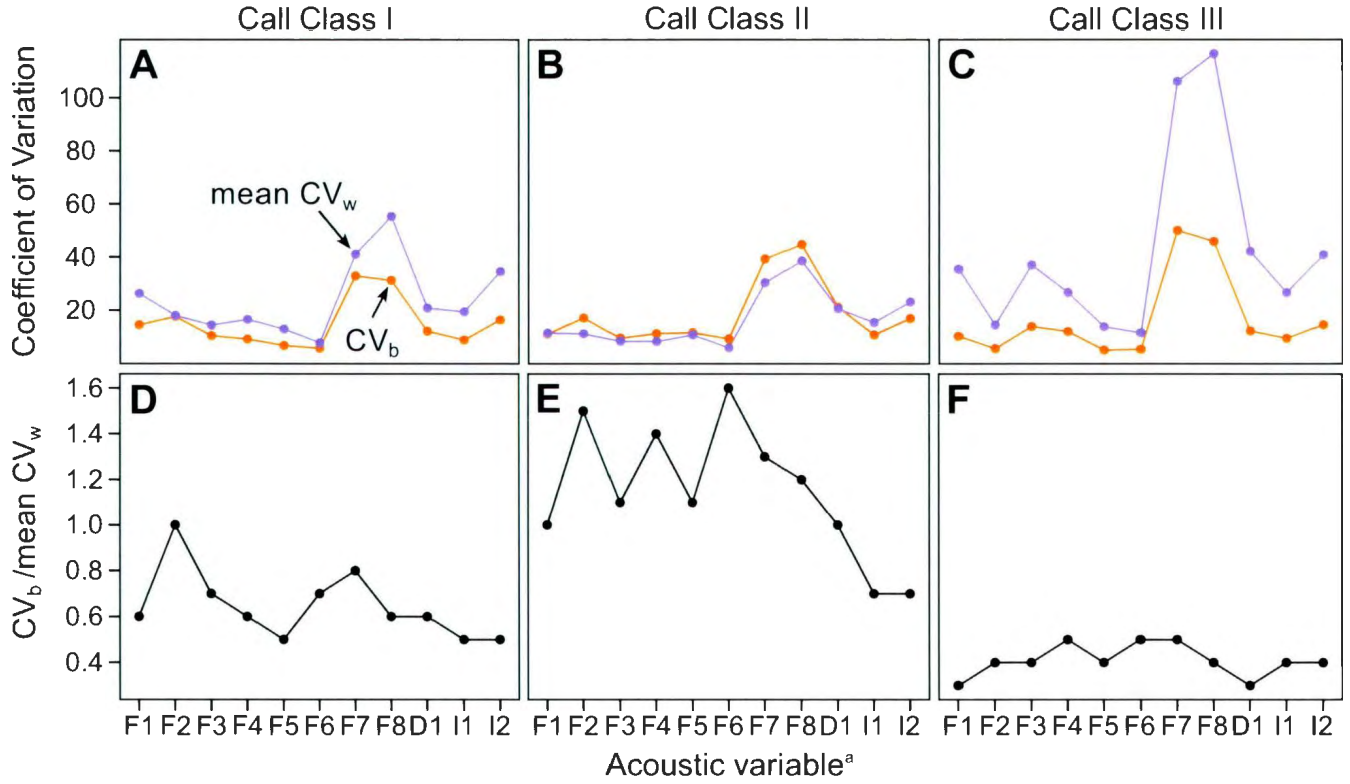

FIGURE 2.8. (A–C) Variability profiles based on recordings of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Variability profiles for call variables are shown for between-individual variation (CV_b; orange line) and the mean CV of call variables within individual adult Red Crossbills (mean CV_w; purple line). (D–F) High variation between birds relative to variation within birds (i.e., CV_b/mean CV_w ratios > 1.0) suggests that Call Class II may contain important information about individual identity; Call Class III showed the least individuality. [a]F1: Frequency at start; F2: Frequency at end; F3: Minimal frequency; F4: Maximal frequency; F5: Frequency at maximal intensity; F6: Mean frequency; F7: Mean absolute slope; F8: Frequency difference between F4 and F5; D1: Duration; I1: Maximal intensity; I2: Intensity at maximal frequency; descriptions of variables are in Table 2.3.

Call Class descriptions. Classification of Call Classes via multivariate analyses corresponded closely to categorizations made subjectively in the field and in the lab with spectrograms. Spectrograms of vocalizations from some individuals that were not corroborated by multivariate clustering showed that these calls were similar to those of other Classes. One misclassified individual, however, was distinct in both call shape and measurements, and may represent a different vocal type (Chapter 3). Despite some discrepancies, multivariate and spectrographic classifications were very similar so I based the following descriptions on the latter (Table 2.4).

Call Class I (Figs. 2.9–2.12). These are common calls of adult Red Crossbills and I recorded them in several different behavioural contexts, such as while perched in tree tops, in flight, or while foraging (Table 2.1; Fig. 2.9). These calls were frequency modulated and tonal, and typically featured harmonic stacks (Fig. 2.10). Thirteen of 14 birds did not differ in any of the 10 acoustic variables across contexts (i.e., in flight vs. perched) and one bird showed only three differences (Appendix: Table A.1). However, pauses between calls from perched birds averaged longer (Fig. 2.11).

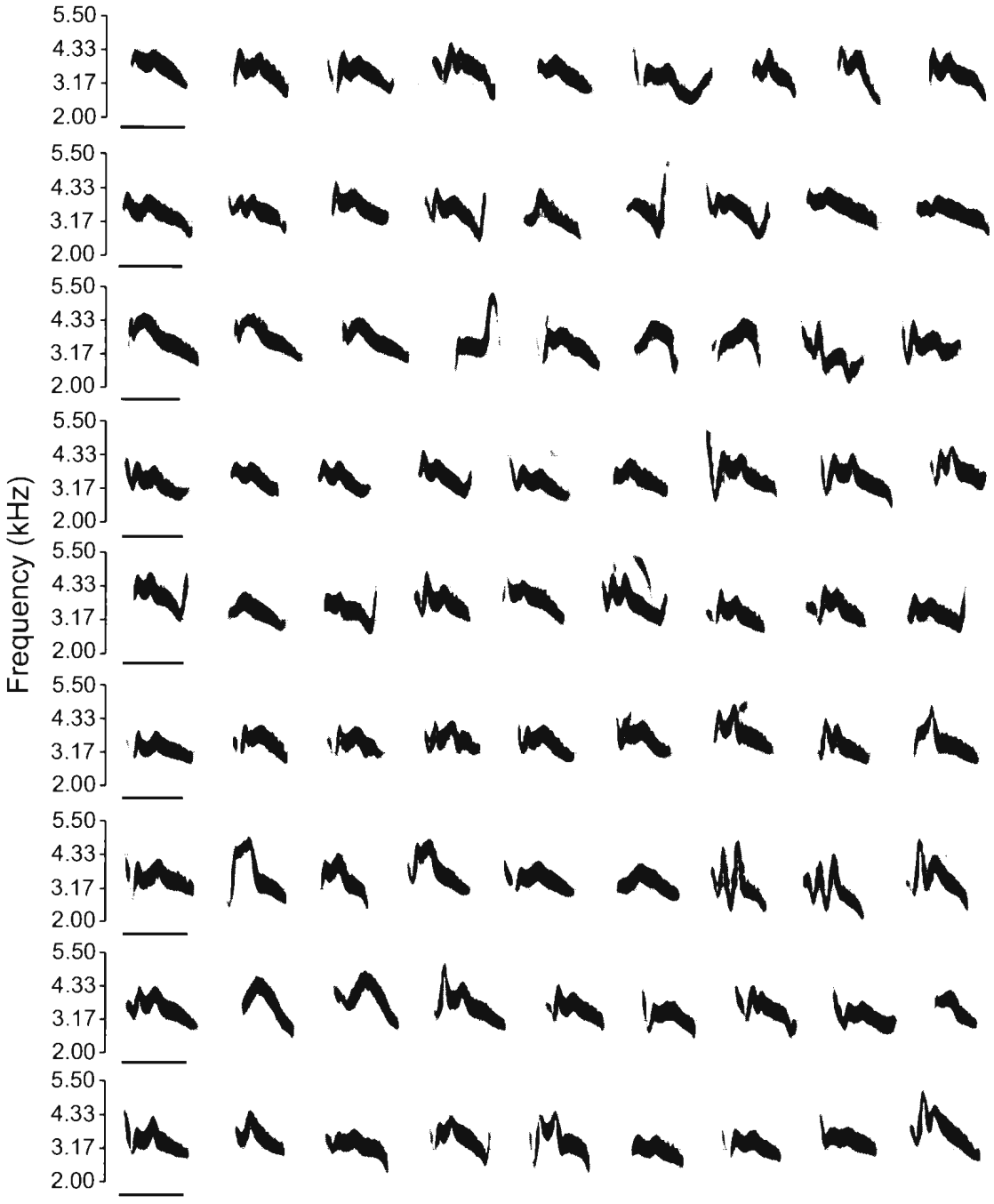

FIGURE 2.9. Examples of Class I calls from 81 adult Red Crossbills (*Loxia curvirostra*; one spectrogram per individual) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Time markers, 50 ms.

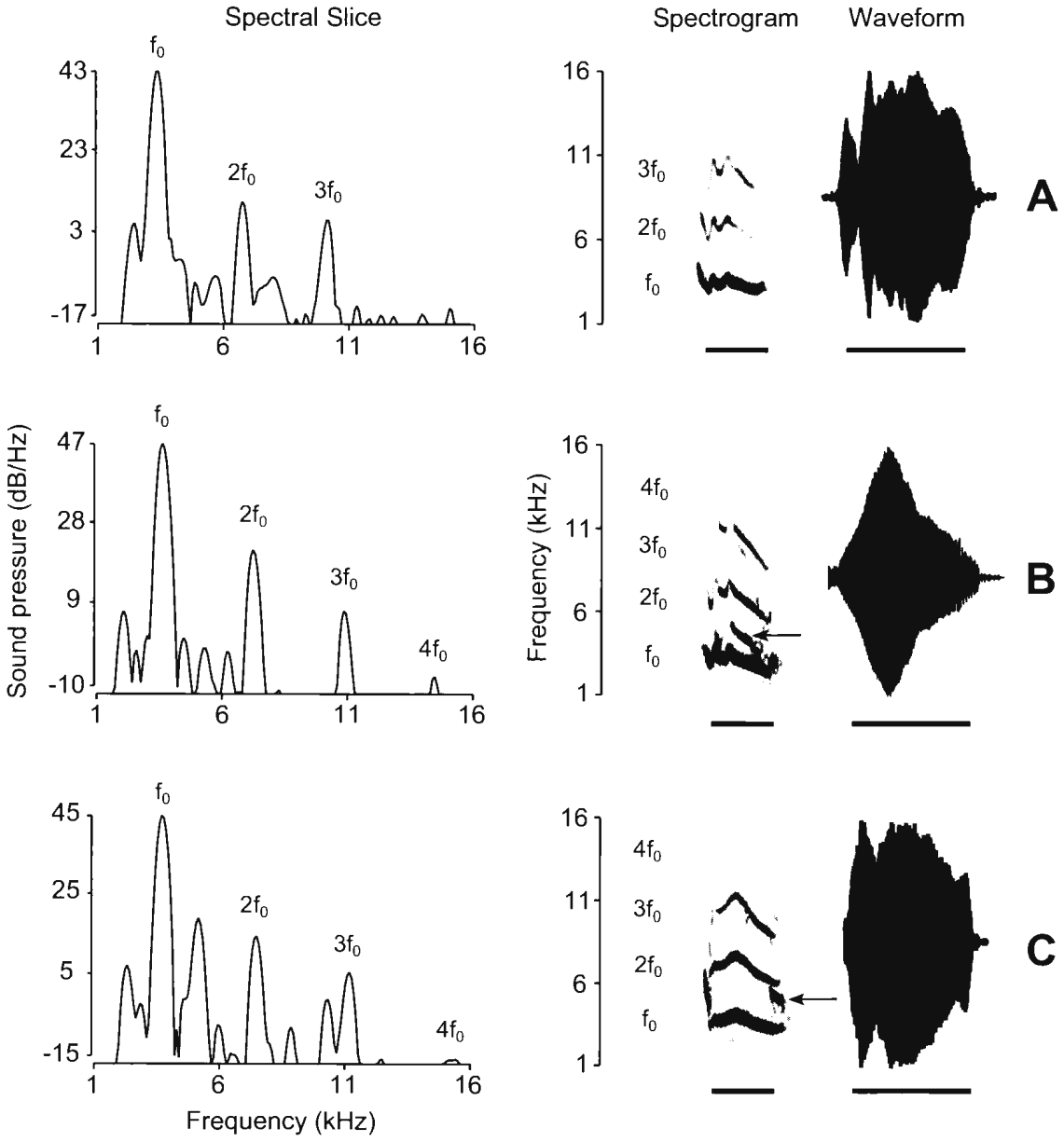

FIGURE 2.10. (A-C) Spectral slices, spectrograms, and waveforms of Call Class I exemplars from three individual Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Calls typically had 3–4 harmonics and some individuals exhibited biphonation (arrows on spectrograms for birds B and C). Small and large bars span 50 ms.

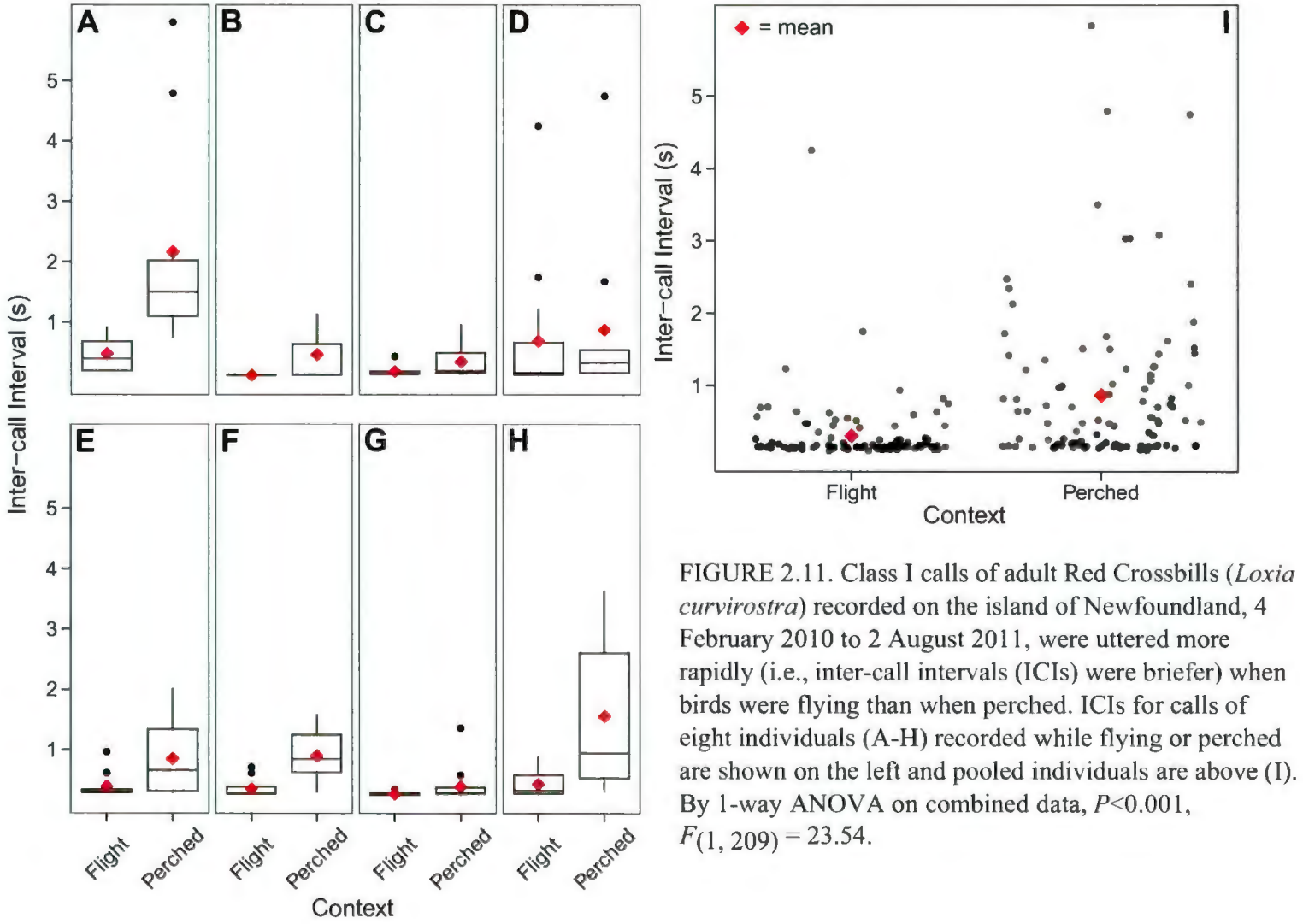

FIGURE 2.11. Class I calls of adult Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011, were uttered more rapidly (i.e., inter-call intervals (ICIs) were briefer) when birds were flying than when perched. ICIs for calls of eight individuals (A-H) recorded while flying or perched are shown on the left and pooled individuals are above (I). By 1-way ANOVA on combined data, $P<0.001$, $F_{(1, 209)} = 23.54$.

Class I calls possessed some amplitude modulation (AM); intensity of the call usually peaked around the midpoint of the call. AM and frequency modulation (FM) were inversely related in some calls (Fig. 2.12A, 2.12F). Calls with rapidly ascending or descending components at the onset were sometimes given with lower relative amplitudes, with discrete breaks between these parts and the remainder of the call (Fig. 2.12B, 2.12C).

As noted above, individuals emitted acoustically similar sounds within calling bouts; only once did a vocalizing bird change the structure of calls during a sequence (Appendix: Fig. A.1). At least 10 adult male-female pairs produced pair-specific calls ("call matching"; Mundinger 1970, Groth 1993b, Sewall 2008).

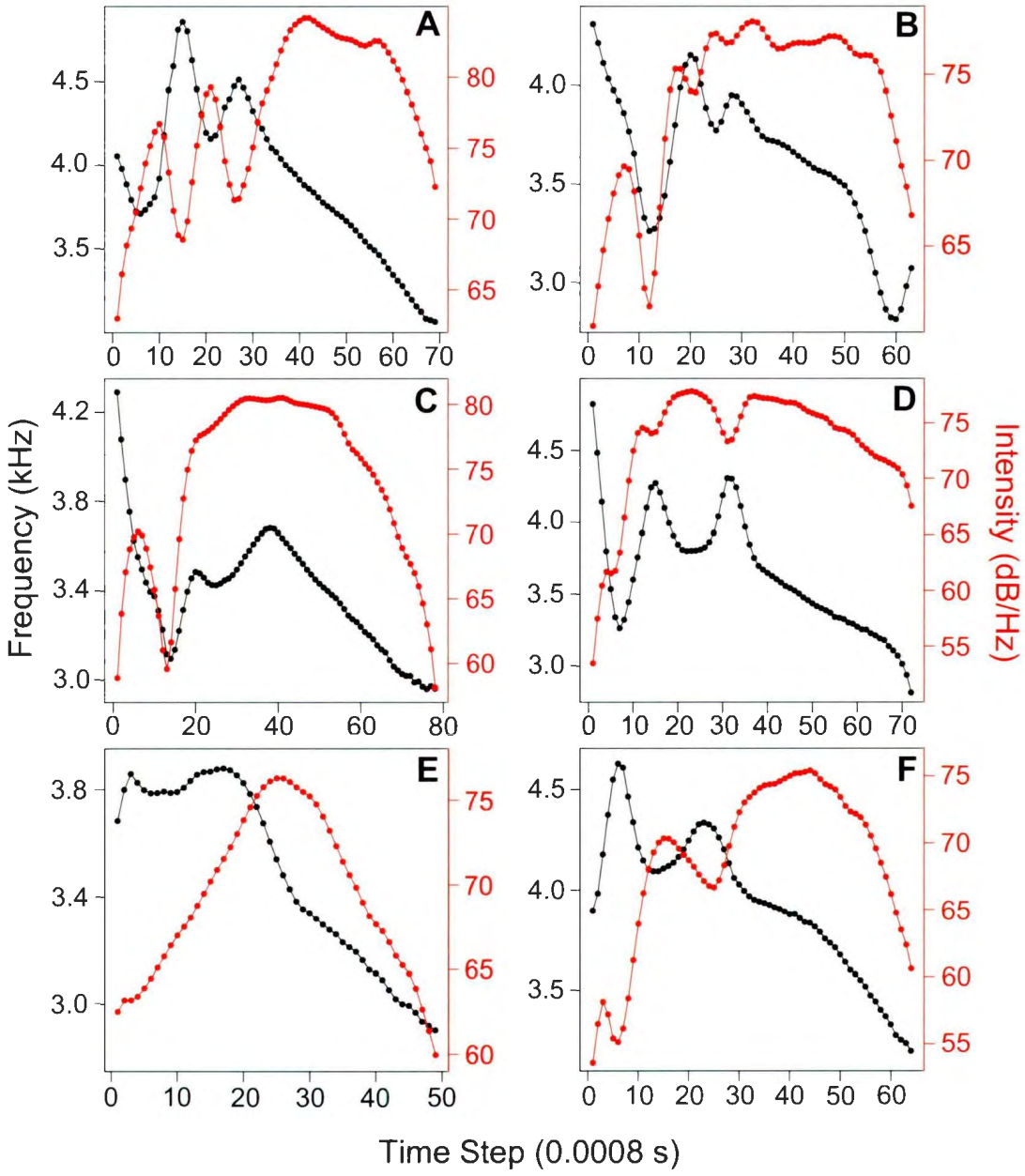

FIGURE 2.12. (A–F) Patterns of amplitude and frequency modulation in exemplars of Class I calls from six adult Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Modulations sometimes were positively and sometimes negatively (e.g., A) correlated. Each panel represents one individual, with frequency and amplitude points representing the mean of five time-normalized calls. Note: frequency in black, intensity in red.

Call Class II. (Figs. 2.13–2.15). Red Crossbills commonly uttered these calls while they foraged (Fig. 2.13). The calls were modulated tones with weak or no harmonics, and were given singly or in series of two to six (Fig. 2.14). Some individuals gave these calls in very rapid series while pivoting or lifting off into flight. Class II calls were given in varied social circumstances such as between apparent mates while moving through forests, or between members of larger foraging flocks, which sometimes included parents and their young. Often these calls were accompanied by "soft whirring of wings" (Robb 2000: 65) as birds fed and moved within conifers or repositioned themselves at bird feeders. Unlike Class I calls, Class II calls were not given by birds in full flight. Class II calls were brief (mean duration = 28 ms) and generally given at low intensity levels (mean = 65 dB/Hz) compared with other vocalizations recorded in this study. Many Class II calls were inaudible at distances of >15–30 m.

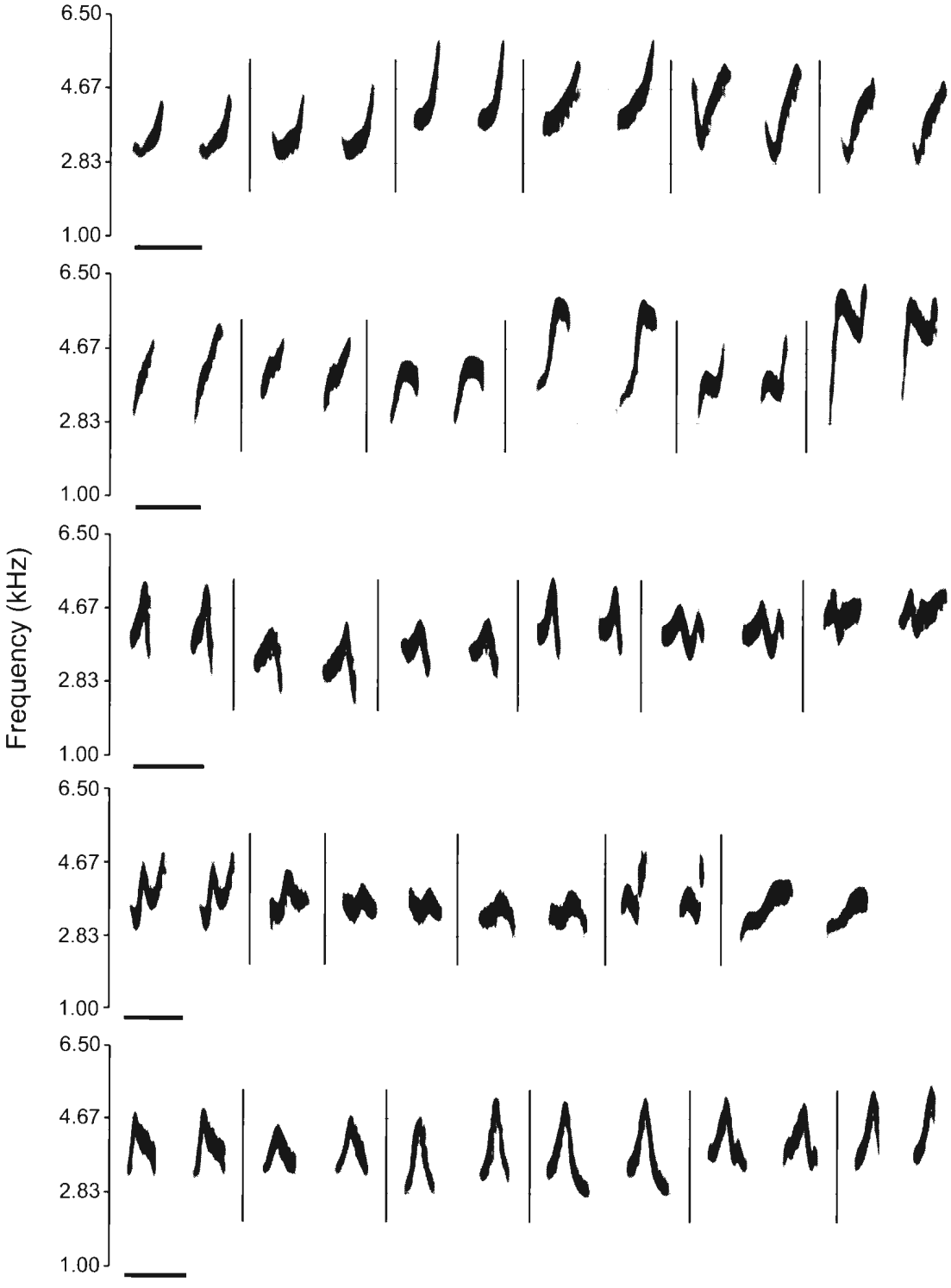

FIGURE 2.13. Examples of Class II calls from 30 adult Red Crossbills (*Loxia curvirostra*; spectrograms from different individuals separated by vertical bars) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Time markers, 50 ms.

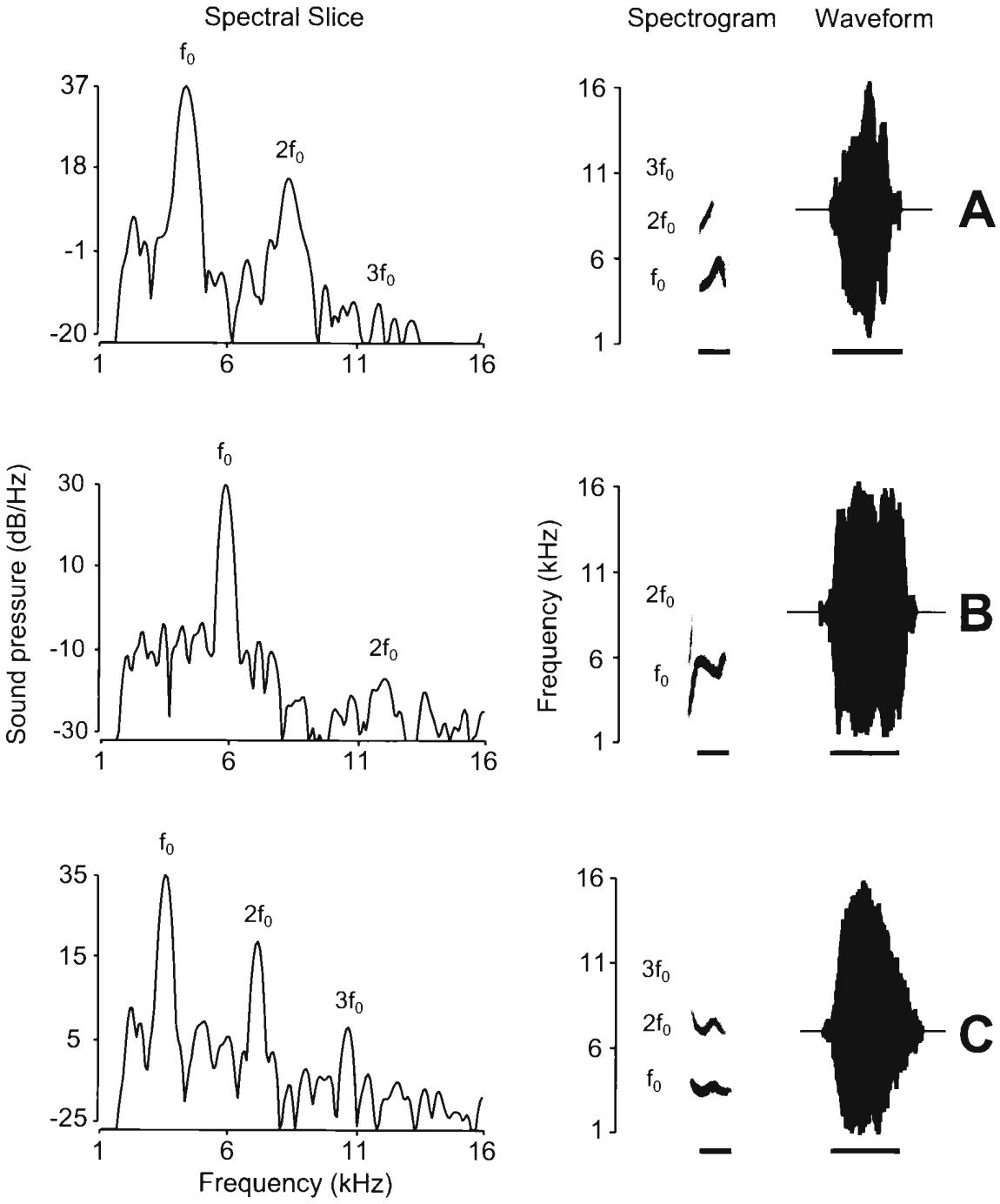

FIGURE 2.14. (A-C) Spectral slices, spectrograms, and waveforms of Call Class II exemplars from three individual Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Calls typically showed 2–3 harmonics; non-linear phenomena were not observed in this Call Class (compare Fig. 2.10). Small and large bars span 25 ms.

Class II calls were highly individualistic and, like Class I calls, intergraded extensively (Fig. 2.15). Such intergradation did not seem to be related to geographic distance, as closely similar calls were sometimes given by birds recorded hundreds of kilometres apart:

1. Two individuals (Howley and Glovertown, separated by ~230 km) gave a high-frequency call, marked spectrographically as a curved, rapidly ascending stroke (Fig. 2.15A).
2. Two individuals (Howley and Whitbourne, separated by ~330 km) emitted similar-sounding calls but these were given at relatively lower frequencies (Fig. 2.15B)
3. Two individuals (Glovertown and Whitbourne, separated by ~150 km) gave chevron-shaped calls (Fig. 2.15C).
4. A Q-shaped call was recorded from several birds at multiple locations (e.g., South River, Clarenville and Howley, separated by ~90–335 km). These calls often were recorded with wing noise as the birds pivoted or made short flights to new perches (Fig. 2.15D).
5. Calls that were somewhat similar-sounding to those of Class I, but were briefer (two individuals from Howley and Clarenville, separated by ~250 km; Fig. 2.15E).

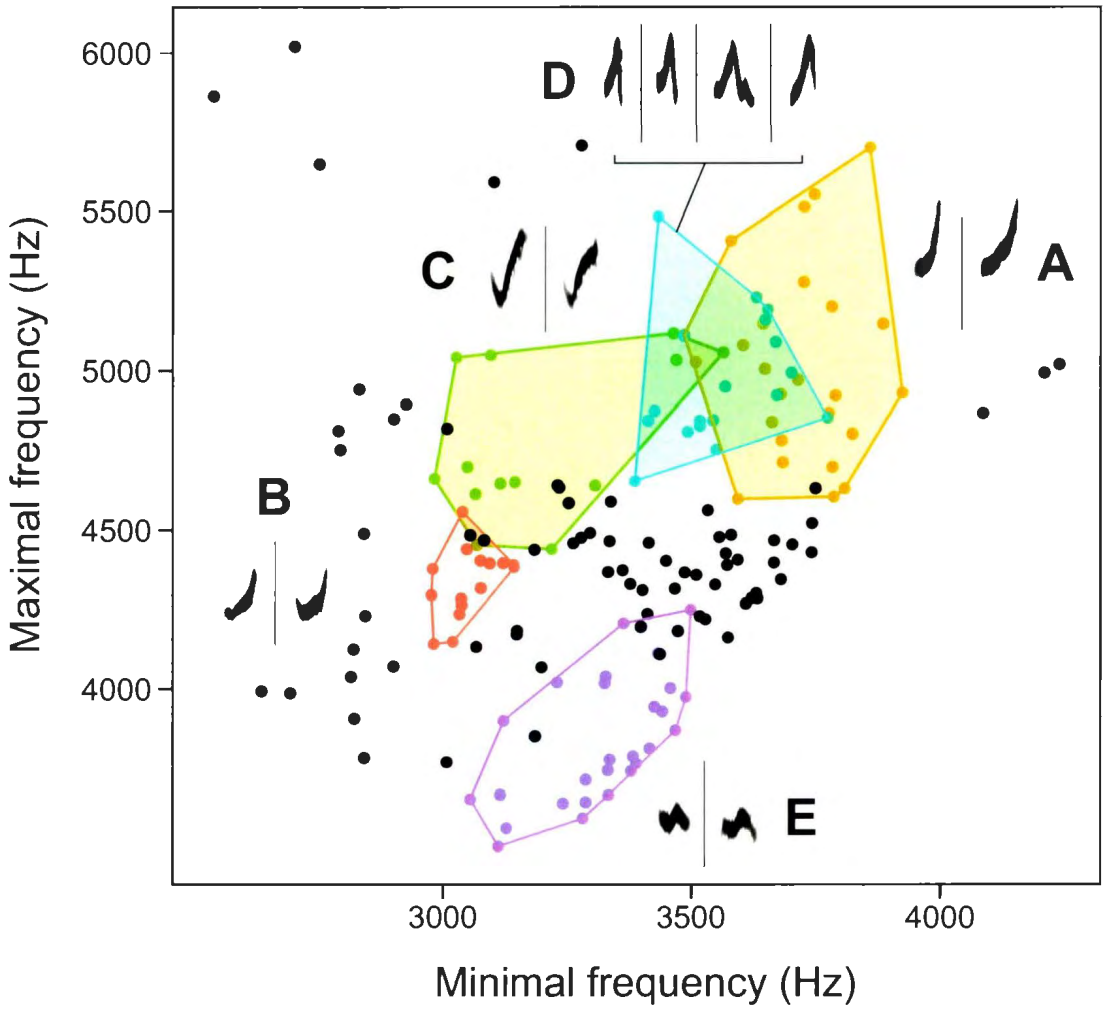

FIGURE 2.15. Grading of Class II calls of Red Crossbills (*Loxia curvirostra*) is expressed in a bivariate plot of minimal and maximal frequencies. The birds were recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Points represent means of different individuals. Five arbitrarily selected groups of birds (A–E) with spectrographically similar calls are shown in different colours, and exemplars from some birds within these groups are shown as spectrographic traces (four birds in group E and two birds each in other groups; bars separating the traces span 2.1–5.4 kHz).

Call Class III (Figs. 2.16–2.17). I recorded these low-frequency, often harmonically rich calls, from birds in varied contexts at nine of the 10 recording sites (Fig. 2.16). Some individuals emitted calls with independent frequency components, a form of biphonation (Fig. 2.17C). These calls seemed to be elicited by the sudden appearance of different heterospecific animals including Osprey (*Pandion haliaetus*), Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), European Starling (*Sturnus vulgaris*), and dog (*Canis familiaris*). In one case, Red Crossbills appeared to use the call as a mobbing signal (Robb 2000): several vigilant perched birds called and other crossbills in the area (~12 adults including both sexes) approached, landed, and called loudly for ~7 minutes apparently in response to a low-flying Herring Gull (*Larus argentatus*). Calls of this Class also were given by a male just before and following an attempt to copulate with a female. Calls of Class III were given only by perched birds and sometimes were inserted into song (see below).

Class III calls differed among individuals on all variables; they also differed statistically across contexts (Table 2.6). However, most variation across variables was attributable to variation within- (19.7–64.7%) and among-individuals (28.0–78.0%), and little (2.3–7.6%) across contexts (singing, vigilant, feeding at bird feeders). Visual examination of spectrograms supported these statistical results; structural differences in calls across contexts were minor.

Nethersole-Thompson's (1975) description of homologous vocalizations in the Scottish Crossbill as low, deep, *toops* applies well to the Class III calls I recorded on the island of Newfoundland. Fundamental frequencies of calls typically were below 3 kHz, making this Class the lowest-frequency sounds recorded. Tall harmonic stacks reaching

14 kHz were sometimes visible in spectrograms but harmonics usually numbered five or fewer (Fig. 2.17).

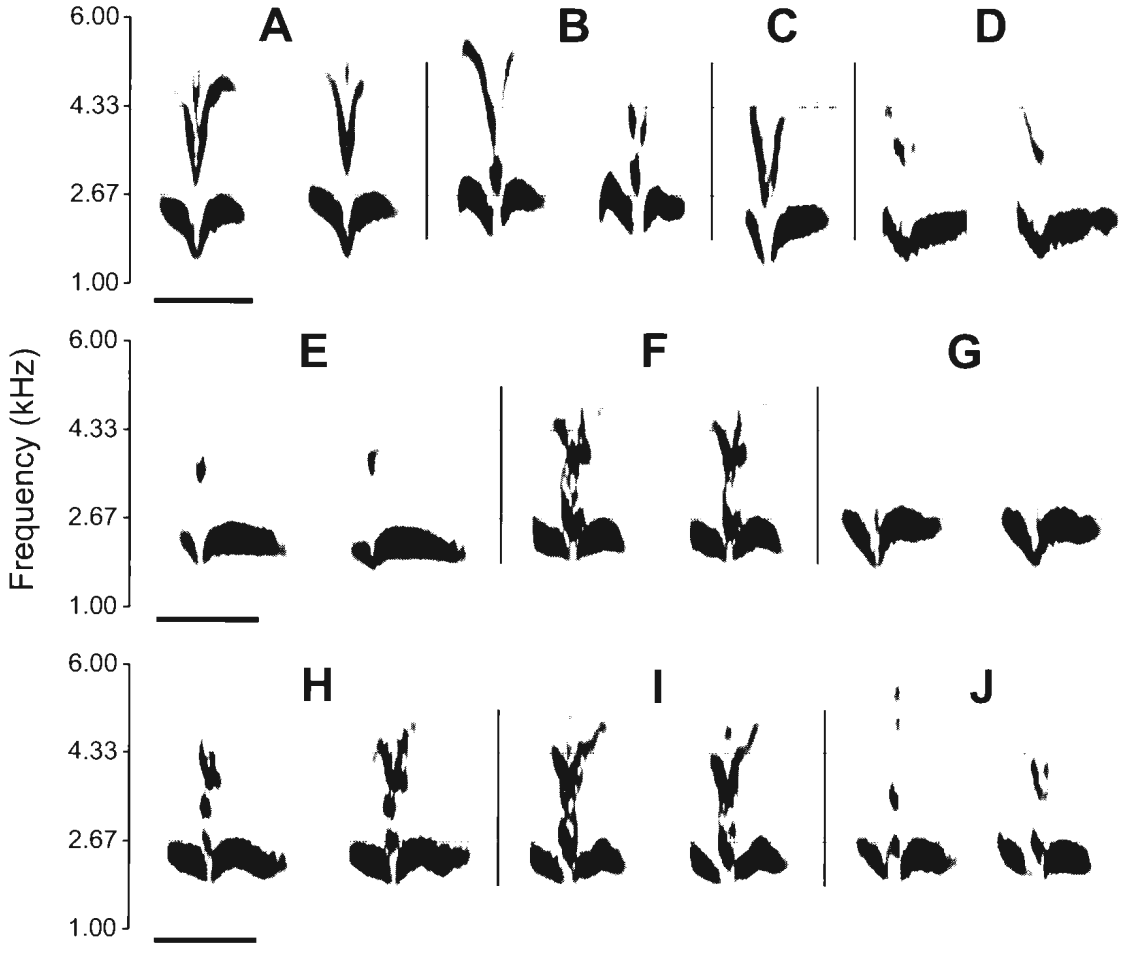

FIGURE 2.16. (A–J) Exemplars of Class III calls from 10 adult Red Crossbills (*Loxia curvirostra*; spectrograms of different birds are separated by vertical bars) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Time markers, 50 ms.

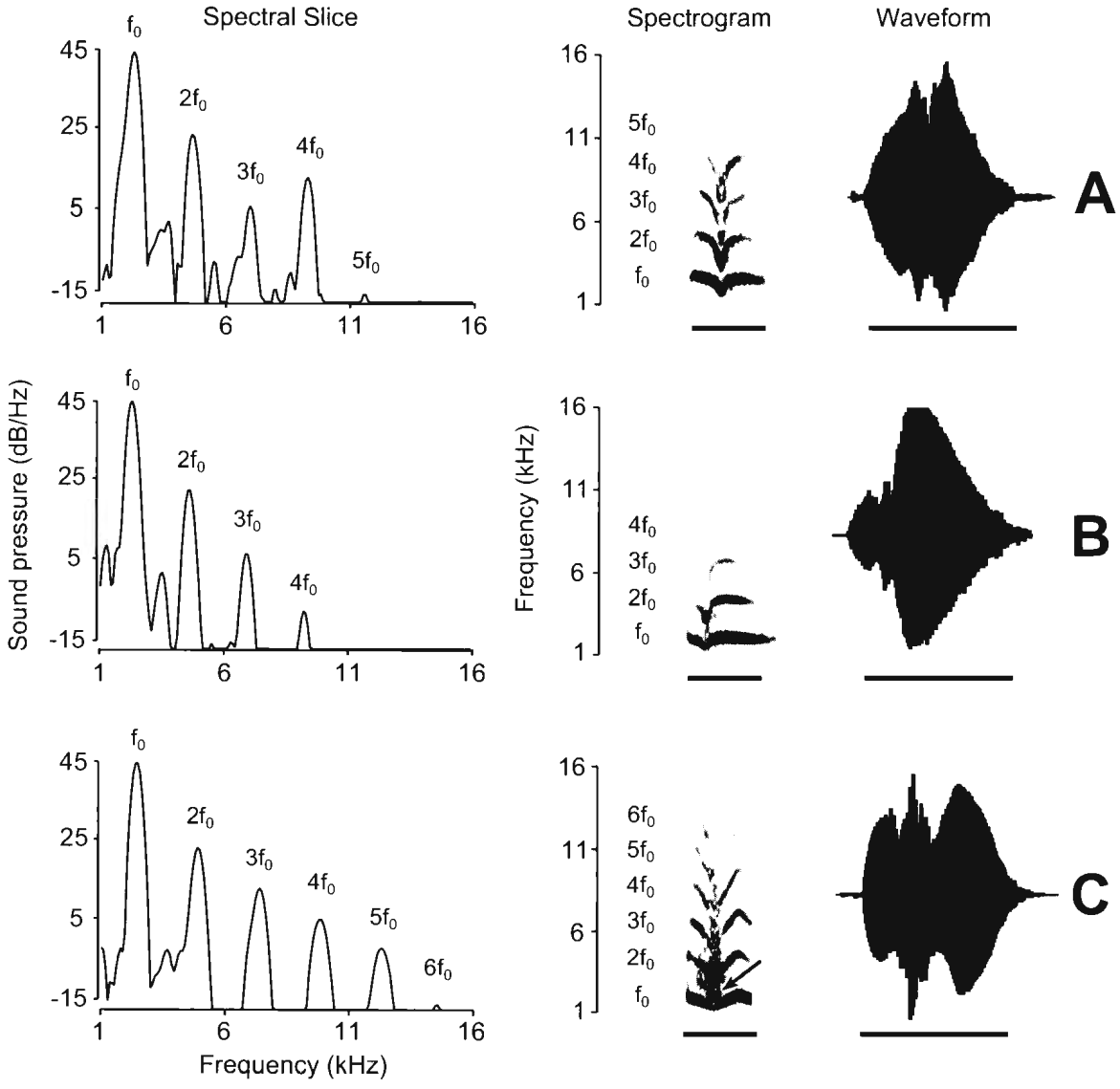

FIGURE 2.17. (A–C) Spectral slices, spectrograms, and waveforms of Call Class III exemplars from three individual Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February 2010 to 2 August 2011. Biphonation (the arrow indicates the second frequency component) and strong harmonics are features of these calls. Small and large bars span 50 ms.

TABLE 2.6. Most variation in Call Class III was attributable to within- and among-individual variation and not to contextual variation. Results of univariate nested ANOVA for 10 variables on Call Class III (n calls = 180) are shown across contexts (singing, vigilant, feeding at bird feeders) and among individuals (n = 17) within contexts. Data are from measurements of calls recorded from adult Red Crossbills (*Loxia curvirostra*) on the island of Newfoundland between 4 February 2010 and 2 August 2011. Figures in **bold** show those variables with significant differences across contexts or individuals after Bonferroni correction ($\alpha' = \alpha/10 = 0.005$); P-estimates are in footnotes.

	Acoustic variable[a]									
	F1	F2	F3	F4	F5	F6	F7	D1	I1	I2
ANOVA										
Among contexts ($F_{3, 169}$)	**14.8**[b]	4.9[c]	0.62[d]	**7.5**[b]	**9.5**[b]	2.5[e]	**8.4**[b]	0.85[f]	**127.4**[b]	**31.9**[b]
Among individuals ($F_{15, 169}$)	**4.5**[b]	**7.7**[b]	**11.3**[b]	**7.7**[b]	**8.3**[b]	**11.9**[b]	**10.7**[b]	**4.8**[b]	**22.6**[b]	**11.6**[b]
VARIANCE COMPONENTS										
Among contexts	6.7	5.9	5.3	7.5	5.5	5.5	7.6	7.3	2.3	5.4
Among individuals	37.0	44.4	49.5	28.9	48.0	48.0	28.0	31.0	78.0	49.3
Within individuals	56.3	49.7	45.2	63.6	46.5	46.5	64.4	61.7	19.7	45.3

[a] F1: Frequency at start; F2: Frequency at end; F3: Minimal frequency; F4: Maximal frequency; F5: Frequency at maximal intensity; F6: Mean frequency; F7: Mean absolute slope; D1: Duration; I1: Maximal intensity; I2: Intensity at maximal frequency; descriptions of variables are in Table 2.3.
[b] $P < 0.001$; [c] $P = 0.008$; [d] $P = 0.54$; [e] $P = 0.08$; [f] $P = 0.43$.

Call Class IV (Figs. 2.18–2.19). Heavily streaked juveniles (21 individuals in total) were observed and recorded at three sites between April and June 2011, and June and July 2012. On a few occasions, juveniles were recorded singing plastic song and uttering notes that resembled Call Classes I and II. More often though, juveniles uttered a loud, strident call (sounds like *chitoo*; Nethersole-Thompson 1975) as they followed adults around foraging areas (Fig. 2.18). I also heard juveniles making these calls, sometimes with quivering wings, while being fed by adults. The calls were structurally complex and commonly featured non-linear phenomena: biphonation, with two independent fundamental frequencies occurring simultaneously across the spectrograms as bands, and subharmonics (Fig. 2.19). As others have noted (Groth 1990, Robb 2000), these calls are variable in duration and frequency, and are generally given with regular cadence. The first call in a sequence often was of higher frequency than other calls in a series, and increased rapidly in frequency (Fig. 2.18A–E). The other calls typically declined smoothly in frequency but varied patterns of FM also were common.

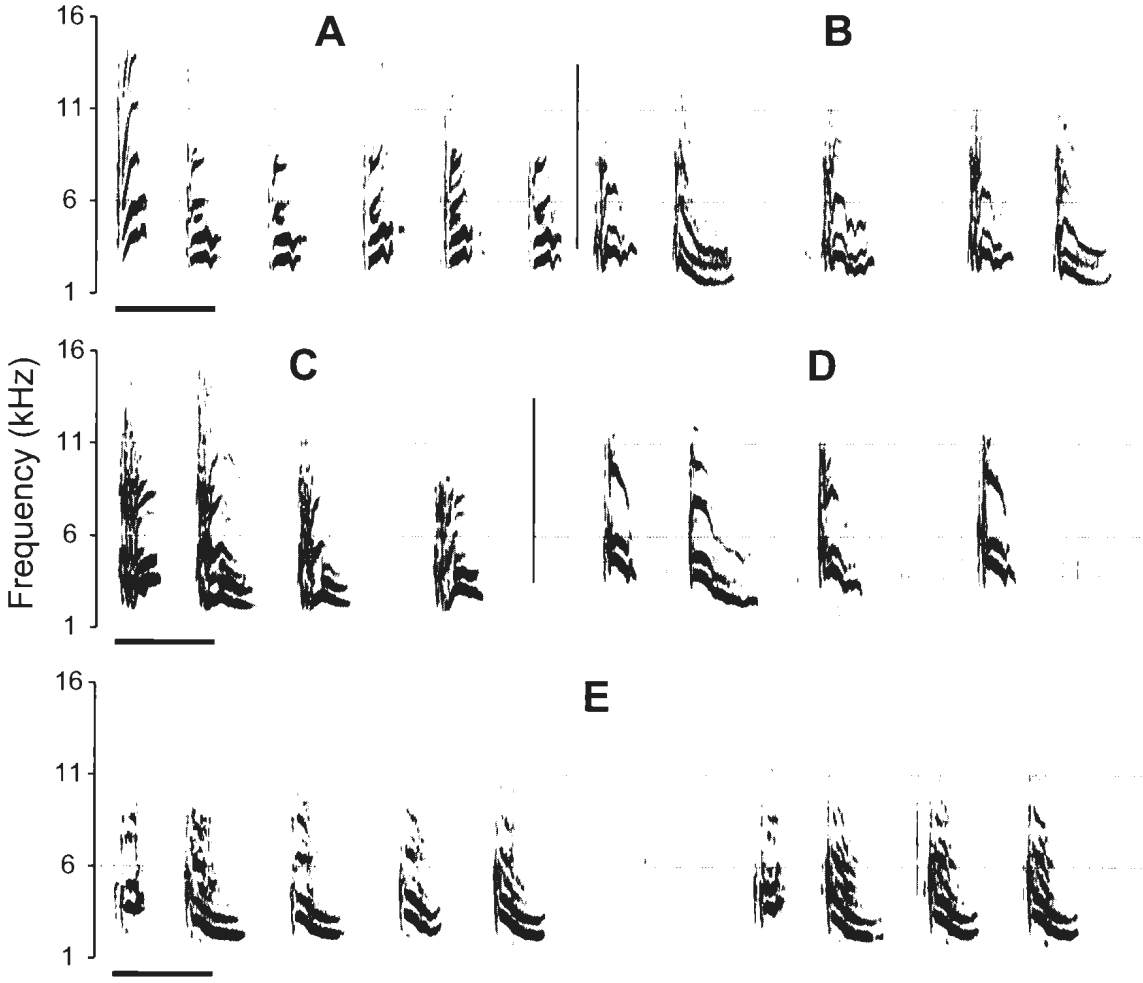

FIGURE 2.18. (A-E) Natural sequences of Class IV calls from juvenile Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland: (A, B) Whitbourne, 17, 24 May 2010; (C, D) West Brook Ecological Reserve, 30 June 2011; and (E) Conception Bay South, 11 June 2011. Bars separate individual birds (n = 5). Time markers, 200 ms.

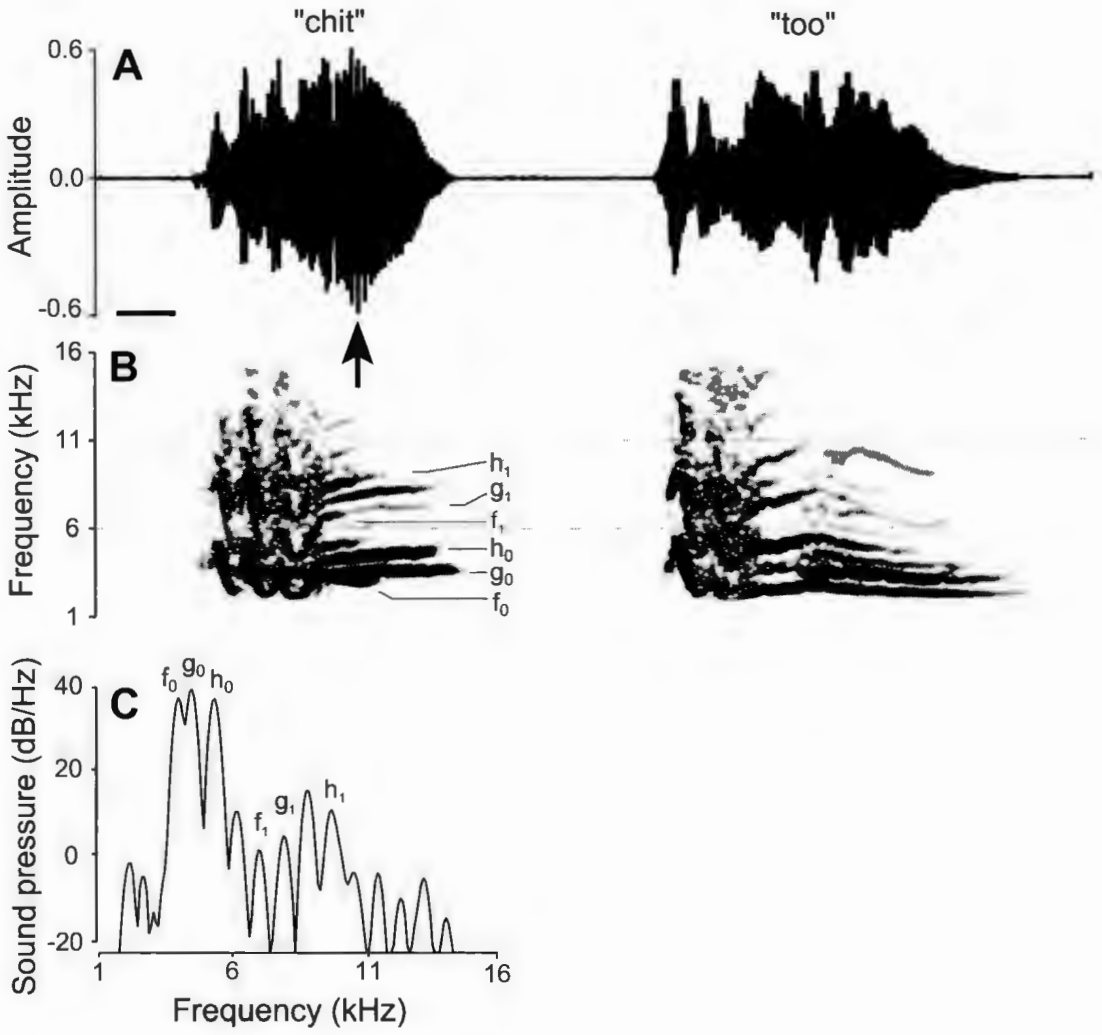

FIGURE 2.19. Waveforms (A) and spectrograms (B) of a Class IV exemplar (*chit* and *too* notes) recorded from a juvenile Red Crossbill (*Loxia curvirostra*) on the island of Newfoundland (West Brook Ecological Reserve, 30 June 2011). The spectral slice (C) is taken from the chit note in A at the maximal intensity of the call (marked by arrow). These calls showed strong subharmonics and biphonation (independent fundamental frequencies are f_0, g_0 and h_0). Time marker, 10 ms.

Call Classes V and VI (Fig. 2.20). Calls of these Classes were harsh and their energy was distributed across a broad frequency band. No obvious harmonics were evident in spectral slices. Both Class V and Class VI (Fig. 2.20A and 2.20B, respectively) were from Red Crossbills fighting for position at bird feeders. Little physical contact occurred during these interactions; however, in one case brief bill-on-bill contact did occur. Juvenile Class V calls had a cadence similar to Class IV calls (Groth 1990). Call class V is was delivered in groups of 3–4 notes; call class VI was given singly and was recorded only once.

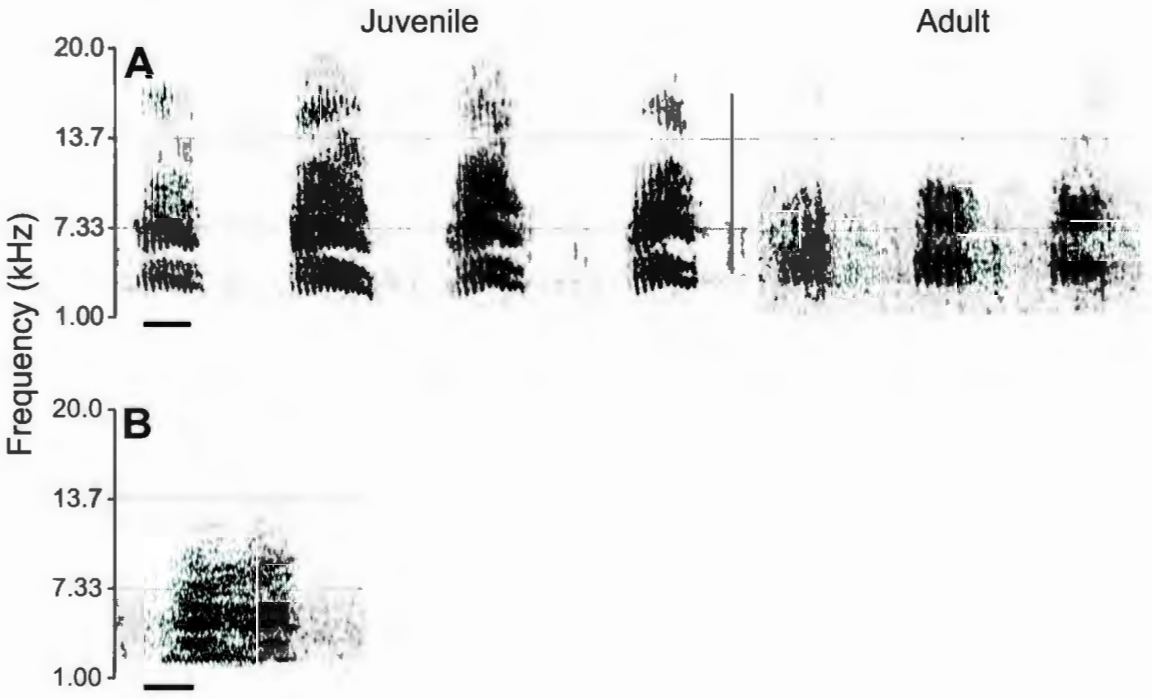

FIGURE 2.20. Call Class V (A) and VI (B) exemplars from Red Crossbills (*Loxia curvirostra*) on the island of Newfoundland, 4 February 2010 to 2 August 2011. Call Class V was recorded on several occasions from both adult and juvenile Red Crossbills as they fought for position with conspecific birds at bird feeders. Call Class VI was recorded only once from an adult in a similar context. Time markers, 50 ms.

Song (Figs. 2.21–2.24). Song comprised varied tonal and noisy components and appeared to be uttered only by adult males, apart from a few juveniles of unknown sex. Male song was delivered in bouts of variable duration (range <1 to > 7 min). I recognized >30 characteristic motifs and notes, some of which are described below. I considered a *motif* to be a group of sounds with a rhythmic or melodic character, and *notes* as single continuous spectrographic traces (Bondesen and Davis 1966). Syllables are groups of two or more notes forming more or less coherent units (Baptista 1977). Single motifs were sometimes repeated to form song (see below).

Song Motif 1 (Fig. 2.21). Some birds sang a relatively brief song that consisted of a single motif repeated several times. All observed instances of this type of song were uttered by perched birds except once (an individual flying overhead). Songs consisting purely of Motif 1 were briefer than songs that combined a number of different motifs and notes. This motif, ~1.6–1.9 s in duration, consisted of up to three of the following note types (Fig. 2.21): (i) a very brief note (mean duration = 14 ms long; SD = 3.6 ms, n = 7); (ii) a longer more complex syllable that descended gradually in frequency (mean duration = 79 ms long; SD = 2.3 ms, n = 9); and (3) a buzzy trill (mean duration = 272 ms, SD = 44 ms, n = 12). Each individual (n = 5) produced its own version of this motif by combining 2 or 3 of the described notes in a distinct sequence.

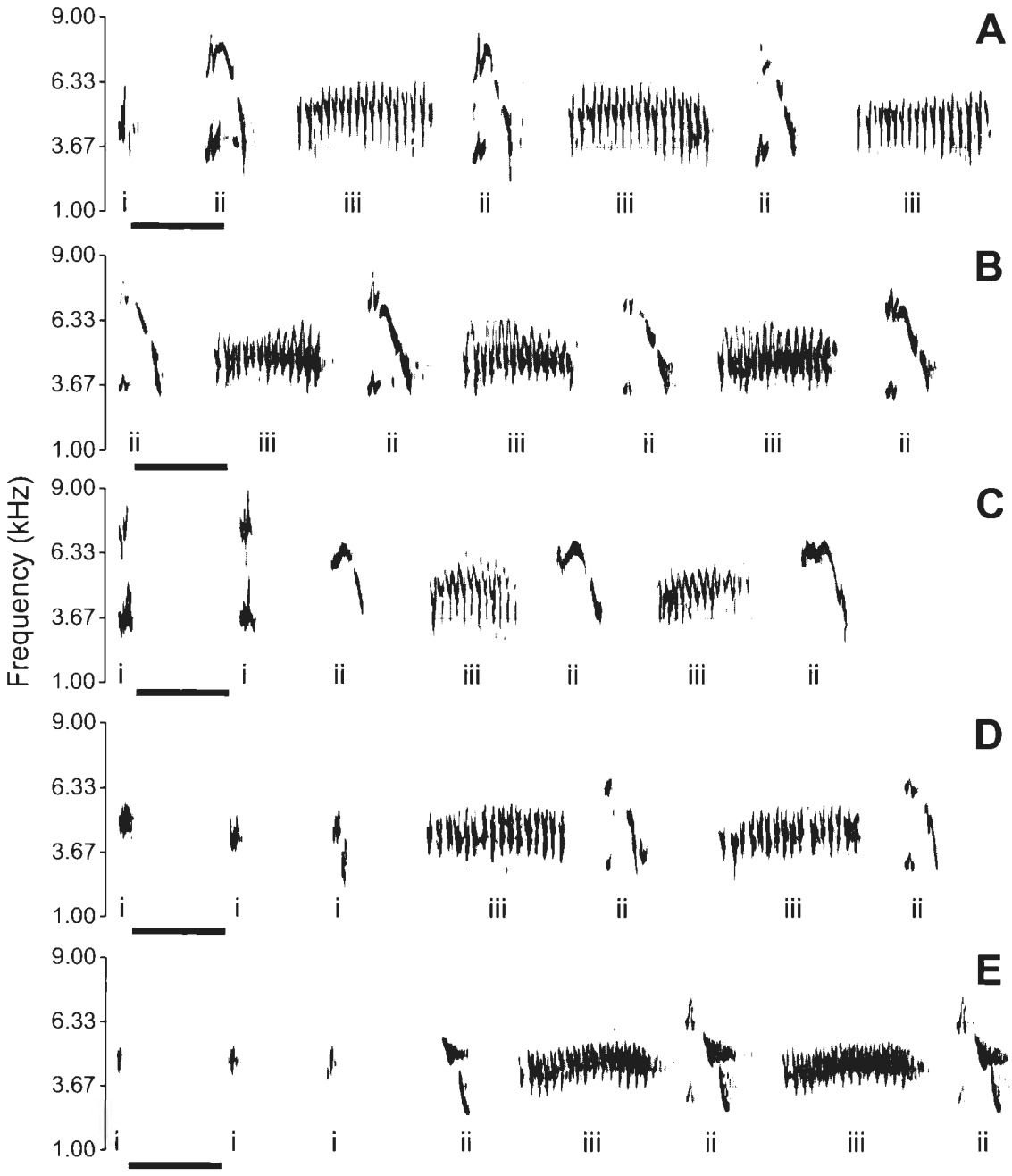

FIGURE 2.21. (A–E) Examples of Song Motif 1 from five different adult male Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland. This motif typically consisted of three types of notes (i: a brief tonal note; ii: a longer tonal note; iii: a trill). Motif 1 averaged 1.8 s in duration (n = 5, SD = 0.11 s). The motif was repeated just by itself or was integrated within longer more complex song. Recordings were from: (A) Conception Bay South, 4 Feb 2010; (B) La Manche, 7 July 2011; (C) Howley, 1 June 2010; (D) South River, 8 June 2011; and (E) Upper Gullies, 21 June 2011. Time markers, 200 ms. All spectrograms show natural sequences.

Song Motif 2. This song was given by males on two occasions while pursuing or interacting with females. In some cases, males uttered songs with Motif 2 while on the wing, hovering near females with exaggerated wing-beats ("butterfly flight"; Hinde 1955, Robb 2000). On other occasions, Motif 2 was integrated within longer and more complex song (consisting of > 25 notes) of perched birds. In flight, 6–7 notes of Motif 2 were uttered as a series; perched birds uttered them in groups of 2–4. The notes were distinctive in structure with a sharp rise in frequency followed by a sharp drop (resulting in an "A-shaped" spectrogram; Fig. 2.22); the frequency range was 1.6–8.0 kHz. Most energy in the note was contained in the descending portion of the call. The notes averaged 102 ms long (SD = 14.8 ms; $n = 43$), were sometimes bisyllabic, and were delivered rapidly (mean ICI = 97 ms; SD = 17.7 ms, $n = 11$).

Sounds similar to those of Call Classes I and III were often used as song elements (Fig. 2.23). As in non-singing contexts, calls of these Classes typically were delivered in pairs and triplets with ICIs averaging slightly longer that the values summarized in Fig. 2.4 (mean ICI of calls in song similar to Class I = 171 ms, SD = 19.6 ms, $n = 10$; mean ICI of calls in song similar to Class III = 224 ms, SD = 67.7 ms, $n = 10$). Red Crossbills also sometimes incorporated short series of a stereotypic brief trill into song (Fig. 2.24). These trills resemble Class V but I never observed them outside of song (Figs. 2.20, 2.24). Trills averaged 76 ms in duration (SD = 17.3 ms, $n = 16$) with a mean ICI of 201 ms (SD = 7.8 ms, $n = 3$).

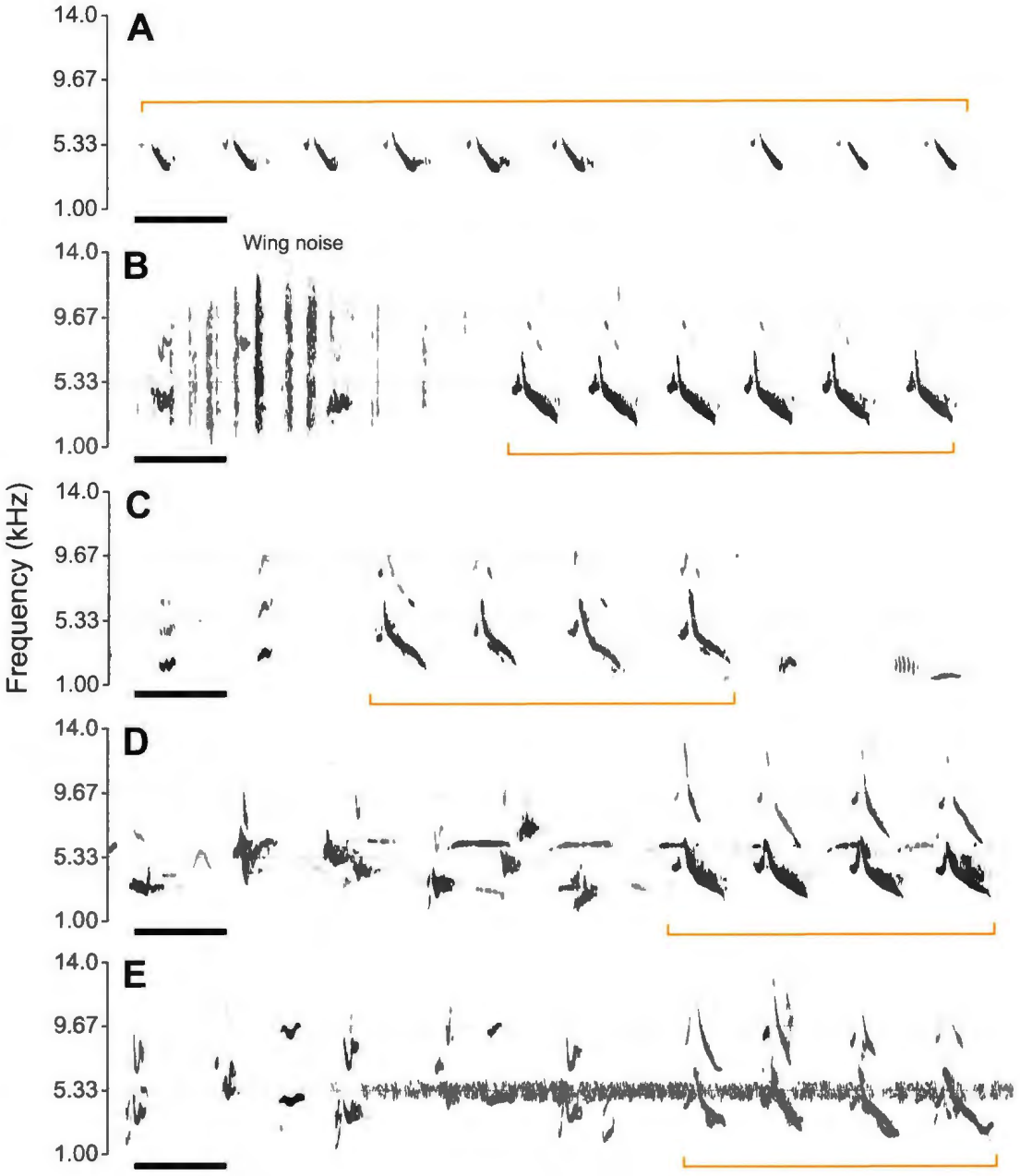

FIGURE 2.22. Song Motif 2 (indicated by orange lines) of male Red Crossbills (*Loxia curvirostra*) was uttered in flight pursuit of or display toward females (A, B). Motif 2 also was inserted into more complex songs by perched birds (C-E). The recordings illustrated here were from five different birds recorded on the island of Newfoundland at: (A) La Manche, 7 July 2011; (B) Goulds, 1 Aug 2011; (C) Conception Bay South, 11 June 2011; (D) South River, 8 June 11; and (E) Upper Gullies, 22 June 2011. Time markers, 200 ms. Spectrograms show natural sequences.

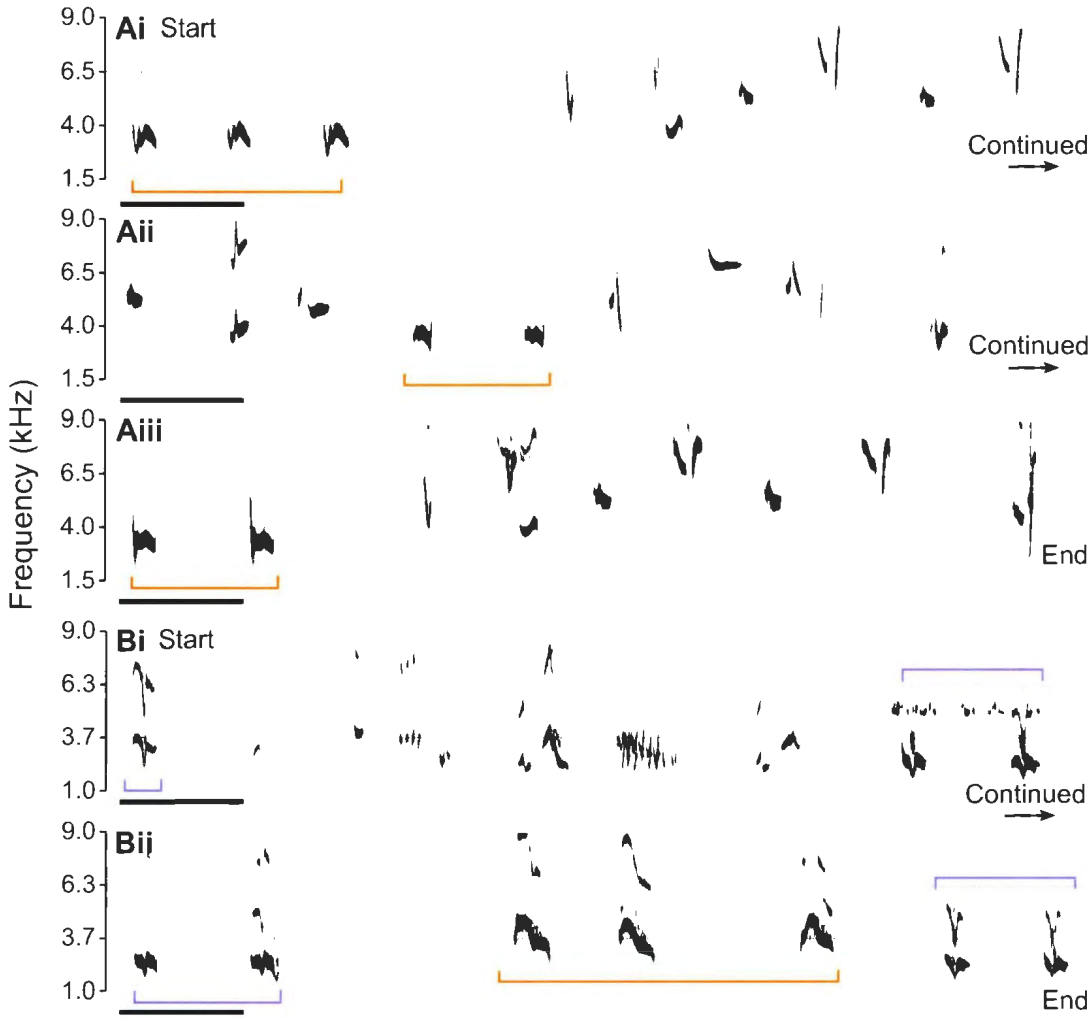

FIGURE 2.23. Calls similar to Classes I and III (indicated by orange and purple lines, respectively) often were integrated within song of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland. Two songs are shown, of durations ~6 s (panels Ai to Aiii) and ~4 s (panels Bi and Bii). Songs from the two males were recorded in: (A) South River, 1 June 2011; and (B) Upper Gullies, 22 June 2010. Time markers, 250 ms.

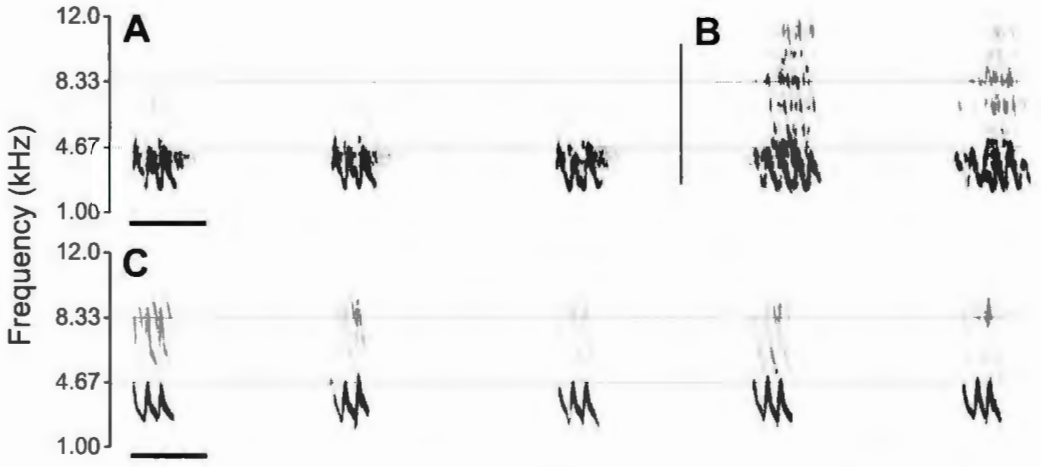

FIGURE 2.24. Songs of male Red Crossbills (*Loxia curvirostra*) from the island of Newfoundland often included repeated brief trills that resembled Class V Calls (Fig. 2.21). Natural sequences from three males (A–C) are shown, recorded from: (A) South River, 8 June 2011; (B) Conception Bay South, 11 June 2011; and (C) Goulds, 1 August 2011. Time markers, 100 ms.

2.4 Discussion

Including song, I established seven vocal categories for Red Crossbills recorded on the island of Newfoundland. Adults uttered Call Classes I–III, V, and VI. Vocalizations from Classes I and II were the most common vocalizations recorded and were given during affiliative interactions, i.e., between apparent mates or by birds in larger groups. Class III was given during both affiliative and agonistic interactions; Classes V and IV were used sparingly and were uttered during interactions between conspecifics. While Classes IV and V were recorded from juveniles, they uttered Class IV calls almost exclusively.

Multivariate quantitative analyses, based on tonal calls (i.e., calls from Classes I–III), produced three Call Classes congruous with classifications made subjectively. In

these analyses, differences in frequency, intensity (i.e., sound pressure levels) and duration of calls were important in distinguishing between Call Classes. In the field, calls from Class I could generally be distinguished from Class II by their relatively lower frequencies and greater overall intensities; however, spectrograms of Class I calls sometimes closely resembled those of Class II calls. Class I calls also contained non-linear phenomena, a feature absent from Class II calls. Class II calls were also shorter in duration and generally had briefer ICIs (but see below). Further, Class II calls were never uttered from birds in full flight, unlike calls from Class I. The low-frequency calls from Class III were the most distinct of all tonal calls in my sample, and were easily distinguishable from other Call Classes by ear and by quantitative analysis. Calls from Classes I–III showed only subtle differences in their ICIs (Fig. 2.4). In a few cases, however, calls from Class II were sometimes recognizable because they were given singly (and softly) with relatively long ICIs (> 2 s), often while birds foraged in tight-knit groups. Classes IV, V and VI also exhibited nonlinear phenomena (i.e., deterministic chaos and subharmonics). Why these nonlinear phenomena occur in acoustic signals is unknown, but communicative roles may include individual discrimination (Volodina et al. 2006) and movement cues (Miller 2002); in some cases, nonlinear phenomena may be non-adaptive by-products of sound production (Fitch et al. 2002). In the harsh-sounding Class IV calls (also known as "begging" calls) nonlinear phenomena may serve to enhance locatability of calling juveniles; these calls feature other qualities that attract the attention of parents, such as wide frequency ranges, abrupt onsets and variable AM and FM (Redondo and De Reyna 1988).

The Call Classes I defined fit well into the vocal categories described for other forms of crossbill that exist elsewhere in continental North America and Europe; all Call Classes have been reported elsewhere (Table 2.1). The general vocal categories are utilized in similar contexts and thus appear to have similar functions across different crossbill forms (Nethersole-Thompson 1975, Groth 1993a, Robb 2000, Irwin 2010). However, my repertoire account is not complete because I did not document calls given by nestlings or in adult-nestling interactions. Further, I did not record other vocalizations such as courtship feeding and copulation calls (see Nethersole-Thompson 1975, Groth 1993a, Robb 2000; however Call Class III was given prior to copulation in one case and in several other cases birds were engaged in courtship feeding but did not vocalize). In addition I did not record "alarm calls" (sensu Groth 1993a). Groth (1988, 1993a), Robb (2000), and Irwin (2010) described "alarm calls" as vocalizations that are structurally similar to "excitement calls." These authors note that "alarm" and "excitement" calls are given in several social contexts, with some apparent overlap (e.g., both names have been used when describing calls uttered by crossbills with potential predators nearby). In my study, Red Crossbill Call Classes generally varied little across contexts. These findings support the idea that a distinction between "alarm" and "excitement" calls may be artificial (Knox cited by Robb 2000:65).

Calls of Class II were the most individual-specific, but some individuals had very similar calls within the Class. Upon further study, these vocal similarities could be found to represent other functional Call Classes that, when analyzed together, appear as a graded system of vocalizations. The level of acoustic variability among individuals in Class II might also suggest that some of the pressures that constrain vocal stereotypy have

been relaxed. For example, since these calls are emitted from crossbills communicating at close range, the use of other non-vocal communicative cues may reduce the need for stereotyped vocalizations that facilitate individual discrimination or the ability to localize (de Kort 2002, Miller and Engstrom 2012).

Singing behaviour has not been well described or documented in North American Red Crossbills, and so it is not known to what degree song is stereotyped within vocal forms. Song is an important indicator of species and population distinctiveness across animal taxa (Payne 1986, Lameira et al. 2010), so Red Crossbill song may contain important taxonomic information that could be specific to different vocal forms. Preliminary investigations into singing behaviour of European crossbills (*Loxia* spp.) suggests that different vocal forms use song in different ways and that distinct song motifs are recognizable across different populations (Robb 2000). In my study, adult crossbills produced at least two distinct song motifs, sometimes sung separately as distinct song types or as elements in more complex song bouts. Motif 1 was sung in a variety of contexts; Motif 2 was sung by males on the wing ("song-flight"; Robb 2000) while aggressively pursuing female Red Crossbills. Classes I and III were also used as song elements. Insertion of these calls into song bouts by individuals may individualize songs and help to facilitate discrimination of signallers by receivers. The use of Class III in song is particularly interesting; outside of song it was often recorded from crossbills when potential predators were apparently perceived. Males who insert this call in song may be attempting to seek attention from breeding females ("attention grabbing"; Reby and Charlton 2012).

Class I and III calls have been recognized widely as species-specific crossbill calls (Groth 1993a, Summers et al. 2002) or as calls diagnostic of different crossbill vocal groups (Robb 2000, Summers et al. 2002, Förschler and Kalko 2009, Irwin 2010). In my sample, Call Classes I and III appear to be representative of a unique Red Crossbill form, possibly *L. c. percna* (Chapter 3). Calls from Classes I and III do not appear to vary acoustically across contexts and generally show a common structural plan among individuals; however, considerable variation in FM is apparent in Class I calls relative to those of Class III. Nevertheless, acoustic variation within both of these Call Classes does not appear to reduce their potential taxonomic value. While Call Class II has not been studied in-depth in other *Loxia* forms, work by Irwin (2010) suggests that there are consistent differences between vocal groups. Further documentation and description of Call Class II in other populations would help assess both their communicative meaning and taxonomic value.

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CHAPTER 3. MULIPLE VOCAL TYPES OF RED CROSSBILL (*LOXIA CURVIROSTRA*) OCCUR ON THE ISLAND OF NEWFOUNDLAND, CANADA

3.1 Introduction

Biologists have long recognised the value of acoustic signals in systematics, for example in discovery or delimitation of new species or to investigate speciation (Lanyon 1969, Payne 1986, Kroodsma and Miller 1996, Martens 1996, McCracken and Sheldon 1997, Alström and Ranft 2003, Lameira et al. 2010). Acoustic signals often are specific to species, populations and individuals, so information about these displays also can shed light on population structure and history, dispersal, the communicative meaning of sounds, etc. (Kroodsma 1974, Naguib et al. 2001, Attard et al. 2010, Summers and Buckland 2010, Filatova et al. 2012, Reby and Charlton 2012). In taxonomic studies, acoustic signals sometimes explain patterns of genetic variation among populations better than do plumage or geography (Rheindt et al. 2008, Rendell et al. 2012; but see Raposo and Höfling 2003). Acoustic signals are used increasingly to detect or identify cryptic species (Alström and Olsson 1999, Zimmermann et al. 2000, Konrad and Geissmann 2006, Braune et al. 2008, Esser et al. 2008, Toews and Irwin 2008, Burton and Nietsch 2010, Lehtinen et al. 2011), defined as "two or more [morphologically similar] species classified as a single nominal species" (Bickford et al. 2007:149). Knowledge of cryptic species can challenge our perceptions about patterns of biological diversity and can have important implications for conservation efforts (Ceballos and Ehrlich 2009, Trontelj and Fišer 2009). For example, the distributions and ecological requirements of newly discovered cryptic species may need re-evaluation, as will any existing conservation strategies associated with the original species complex (Rutishauser et al. 2012).

Discovery of these "species within species" poses a challenge in itself. Besides accruing genetic evidence, systematists must discover and document non-traditional (i.e., non-morphological) species-specific characters such as chemical or acoustic signals (Bickford et al. 2007).

Vocalizations of the Red Crossbill (*Loxia curvirostra*), a cone-obligate, seed-eating specialist of Holarctic forests, offer a non-invasive tool for diagnosis and discrimination of cryptic forms (Groth 1988, 1993a). Morphological and ecological variation in crossbills has long confused taxonomists, and various subspecies and classification schemes have been proposed over the years (Griscom 1937, Monson and Phillips 1981, Dickerman 1987). However, in a broad survey of North American Red Crossbill vocalizations, Groth (1993a) found that morphologically and ecologically distinct forms also share distinct calls. A large cryptic sibling species complex was uncovered, triggering further research; other workers have since reported a similar situation for European crossbills (Robb 2000, Summers et al. 2002, Alonso et al. 2006, Constantine and The Sound Approach 2006, Borrás et al. 2008, Förschler and Kalko 2009, Lindholm 2011, Edelaar et al. 2012).

Aside from differing in vocalizations, at least 10 of the North American vocal forms ("types"; Groth 1993a) also differ in body and bill size, anatomy of the palate, and feeding preferences (Benkman 1993, Groth 1993a, Benkman et al. 2009, Irwin 2010). Phenotypic divergence is thought to be recent (within the last 12 000 years) because vocally distinct forms exhibit weak genetic differentiation (Parchman 2007). Nonetheless, there is strong evidence that crossbill vocalizations play an important role in the evolution and maintenance of ecological and morphological variation within crossbill complexes. In

particular, rapid, frequency modulated vocalizations known as "flight calls" appear to function as sexually selected marker traits, containing public information about the ecological status of the calling individual or the flock (Snowberg and Benkman 2007, Edelaar 2008, Smith et al. 2012). Over short-term studies, these stereotypic calls appear to be stable across generations, with young learning the calls of their parents and thus facilitating family cohesion (Sewall 2011). Cohesion among morphologically similar individuals is biologically important because foraging traits (e.g., bill depth) are correlated with cone-type preference (Lack 1944), and feeding performance is optimized when forms feed on cones of particular conifer species ("key conifers"; Benkman 1993, 2010). Further, bill structure is highly heritable (Summers et al. 2007) and studies predict that hybrids between ecologically differentiated forms should be selected against (Benkman 1993, Benkman 2003). In summary, a link between a genetically influenced phenotypic trait (i.e., bill structure) and ecological niche (reflected in cone shape) appears to be present.

Evidence that crossbill populations exhibit mate preferences and mate assortatively on the basis of acoustic cues helps to explain how phenotypic differences could be maintained among sympatric crossbill populations (Benkman 1987, Knox 1990, Groth 1993b, Summers et al. 2007). Range overlap among vocally distinct forms is facilitated by nomadism, which enables the forms to encounter ephemeral, irregularly distributed cone crops of preferred species (Griscom 1937, Alonso and Arizaga 2012). Work on Darwin's finches further supports the notion that vocalizations can serve as a behavioural mechanism for assortative mating in sympatric populations (Podos 2010).

It has long been assumed that only the island of Newfoundland is home to a single well marked form of Red Crossbill, the endemic *Loxia curvirostra percna*. Bent (1912) first described this subspecies on the basis of 11 specimens that he collected in southwestern Newfoundland in the early 20th century. He noted differences in body and bill size from other North American subspecies recognized at the time, and remarked especially on the much darker plumage colours of *percna* (Bent 1912). Other workers have supported the distinctiveness of *percna* and it has generally been assumed that the form is restricted to the island of Newfoundland (Griscom 1937, Burleigh and Peters 1948, Payne 1987, COSEWIC 2004; but see Bent 1920, Dickerman 1987).

Red Crossbills were considered to be common through the first three quarters of the 20th century (Peters and Burleigh 1951, Erskine 1977) on the island of Newfoundland. However, recent Christmas Bird Count data suggest that Red Crossbill numbers on the island have been in decline, possibly due to habitat reduction (COSEWIC 2004). On this basis, *L. c. percna* is currently listed as Endangered in both Provincial and Federal legislation. However, evidence is lacking about: (a) whether *percna* is a biological entity rather than just a taxonomic entity, and if so whether the form still exists; and (b) the possible presence of other cryptic Red Crossbill forms on the island. The purpose of my study was to describe vocalizations of Red Crossbills on the island of Newfoundland and to assess any differences between vocalizations from the island and elsewhere in mainland North America and Europe. I predicted that vocalizations from island birds would differ from mainland populations and would be uniform throughout the island if *percna* and only *percna* is present. If *percna* was not present in samples, I predicted that vocalizations would resemble those described for forms in mainland North

America. Finally, if both *percna* and other forms were present I expected a mixture of vocalizations, some distinctive and previously undescribed: the latter could be from *percna*.

Definition of terms

Type; vocal type. Groth (1993a) originally simply numbered Red Crossbill forms one through eight as he discovered them (Fig. 3.1). As vocal, morphological, and ecological variation among individuals was sorted on the basis of vocal differences, he termed the forms *vocal types*. Here, I use the terms *vocal types/types* to refer to vocally distinct crossbill forms in North America and Europe.

Call Classes. A bird's repertoire consists of a set of vocalizations that are used throughout its life cycle (Marler 2004). I use the term *Call Class* to refer to a set of structurally similar calls; these sets together constitute the vocal repertoire. Varied names have been applied to Call Classes of the Red Crossbill, sometimes onomatopoetically and sometimes in vague or unitary functional terms (e.g., "contact", "excitement" or "social" calls). I avoid the use of such names because they are not descriptive and often imply single functions that have not been established and that merely reflect arbitrary views of different observers. Instead, I employ the use of neutral terms (from Chapter 2) to avoid these problems (Miller 1991, Martin and Bateson 1993): Call Classes I (*chip*, contact call, *dyip*-call, flight call, or travelling call of other workers) and III (excitement call, or *toop* or *tep* of other workers; Bailey et al. 1958, Nethersole-Thompson 1975, Groth 1990, Cramp and Perrins 1994, Adkisson 1996, Robb 2000, Knox cited by Robb 2000:65, Summers et al. 2002, Sewall 2008, Benkman et al. 2009, Irwin 2010). Calls of these two Classes have been used to identify and delimit crossbill vocal forms in other studies (Fig.

3.1; Groth 1993a, Robb 2000, Summers et al. 2002; Benkman et al. 2009; Irwin 2010). Newfoundland birds also emit Class II calls (*chitter*, communication call, contact call, *peep* or *wik* of other workers; Bailey et al. 1958; Nethersole-Thompson 1975; Groth 1993a; Adkisson 1996; Robb 2000; Knox cited by Robb 2000:65; Irwin 2010); these are described in Chapter 2. Class II vocalizations were not included in the comparative portion of this study because, as they have not been targeted for study in other vocal types, recordings are not readily available.

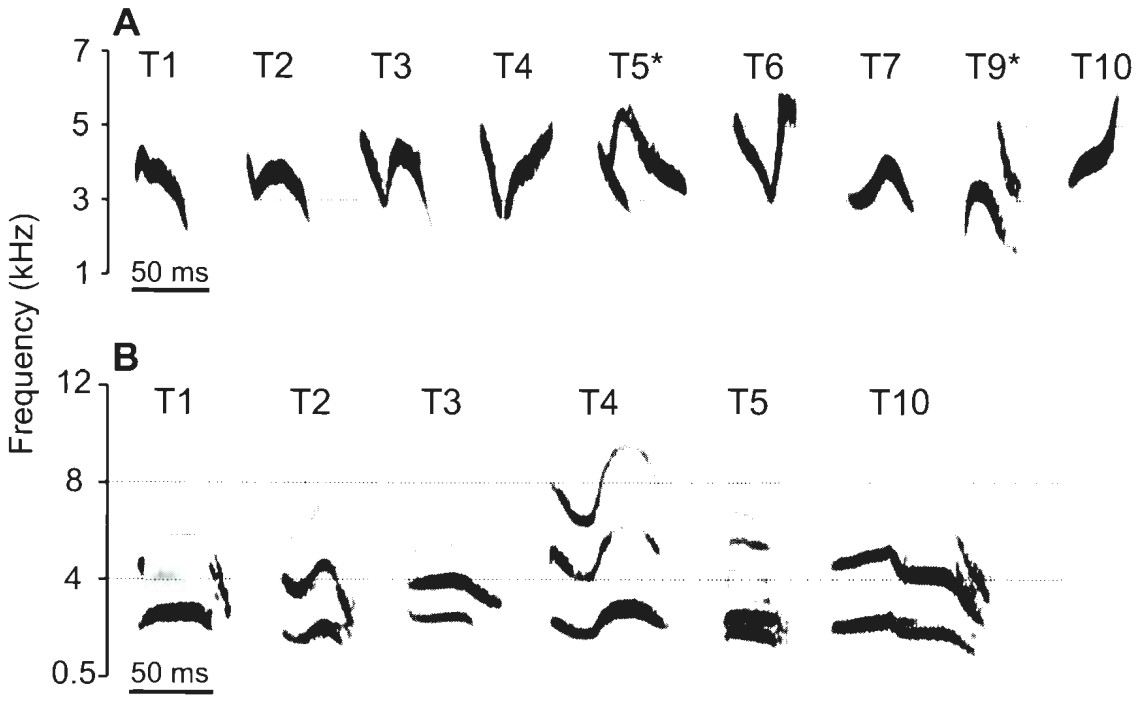

FIGURE 3.1. Representative spectrograms of Class I (A) and Class III (B) vocalizations which have been used in systematic studies of crossbills (*Loxia* spp.). T1–T7, T9, and T10 refer to "types" of North American Red Crossbill (*L. curvirostra*), sensu Groth (1993). Asterisks mark call types that commonly show biphonation (Groth 1993a, Benkman et al. 2009). Class I calls were recorded by J. Groth except: T1, recorded by G. Budney (Macaulay Library, ML # 137497); T9, recorded by T. Brooks (www.xeno-canto.org/38896); and T10, recorded by C. Duncan (Macaulay Library, ML # 112167). Class III calls were recorded by J. Groth except T5 and T10, which were recorded by A. Spencer (www.xeno-canto.org/34777 and www.xeno-canto.org/28868, respectively).

3.2 Methods

Study sites and subjects. Red Crossbills were recorded on the island of Newfoundland, Canada, between 4 February 2010 and 2 August 2011. Recordings and observations were made at 10 localities: Clarenville, Glovertown, West Brook Ecological Reserve, and Howley in central Newfoundland; Conception Bay South, Goulds, La Manche, South River, Upper Gullies, and Whitbourne on the Avalon Peninsula in eastern Newfoundland (coordinates are given in Methods of Chapter 2; see also Appendix Table A.2). Recordings were made with a Fostex FR–LE2 field recorder, a Telinga Pro Series microphone and a 570 mm Telinga parabola. Vocalizations were sampled at 44.1 Hz and digitized at 16 bits.

To collect material for comparison with Red Crossbills from the island of Newfoundland, over 25 hours of archived recordings were obtained from public (Museum of Vertebrate Zoology, University of California Berkeley; Macaulay Library, Cornell University, xeno-canto.org, Project AVoCet (Avian Vocalizations Center), Borror Laboratory of Bioacoustics), private and commercial sources (Robb 2000, Constantine and The Sound Approach 2006, Bergmann et al. 2008). This material was subjected to spectrographic analysis; vocal types and Call Classes were identified and corroborated with corresponding track metadata. From this material, a subset of 245 Class I calls from 31 individuals (Table 3.1) was subjected to discriminant analysis (DA; see below).

Call Classes from original Newfoundland recordings were grouped by ear, appearance of spectrograms and birds' behaviour; subsequent statistical classifications of calls, via multivariate clustering techniques, corresponded closely to the groupings made

subjectively (Chapter 2). This sample consisted of 890 calls from 83 individuals and was also included in the DA.

TABLE 3.1. Summary of recording localities, dates, sample sizes and spectrograms for sound recordings of crossbills (*Loxia* spp.) used in the multivariate analyses.

Locality[a]	Date	*n* Adults (Vocal type[b])	Source[c]
Island of Newfoundland			
Clarenville	2010: 18 February, 26–27 June	7 (2, 8, 10)	this study
Conception Bay South	2010: 4 February, 31 March, 28 April; 2011: June 11, 17, 21	17 (8)	↓
Glovertown	2011: 28–29 January	7 (8)	↓
Goulds	2011: 18 July 1–2 August	10 (8)	↓
Howley	2011: 30 April, 1–2 May	9 (8)	↓
La Manche	2011: 8 July	1 (8)	↓
South River	2011: 1, 8, 10 June	8 (8)	↓
Upper Gullies	2011: 21–22 June	9 (2, 8)	↓
West Brook Ecological Reserve	2011: 30 June	2 (8)	↓
Whitbourne	2010: 17, 22–23 May, 16 July; 2011: 9, 11 March, 13 April, 8 June, 30 July	13 (8)	↓
Mainland North America			
Arizona	1985: 27 July	2 (2)	MVZ 4296
British Columbia	1987: 5 August	2 (3, 4)	MVZ 4743, 4748
British Columbia	1962: 2 June	2 (1)	ML 58169
California	1994: 11 June; 2002: 7 June	4 (2)	ML 106639, 120423
Idaho	1986: 2, 4, 6 August	4 (6, 7)	MVZ 2694, 2702, 2726, 5092
Maine	1998: 16 July	1 (10)	ML 112167
Michigan	1987: 16 July; 2011: 9 April	6 (10, 4)	AV 12830; MVZ 4696, 4692, 4659
New York	2006: 5, 6 August	3 (1)	ML 138310,

			137497
Oregon	1985: 7 June	1 (2)	MVZ 4238
Europe			
Netherlands	1998: 21 February, 14 March; 1999: 13 February	4 (E[d])	Robb (2000): Track 40
Scotland	1983: 18 April	1[e] (*Loxia scotica* or *L. pytyopsittacus*)	Robb (2000): Track 49
Scotland	2002: 20 March	1 (*L. scotica*)	CSA (2006): Track 87

[a]For geographic coordinates and other geographic data see 2.2 Methods (Chapter 2) and Table A.2 in the Appendix.
[b]Vocal types from the island of Newfoundland are based on analyses presented in the Results section of this Chapter.
[c]AV = Avian Vocalizations Center, Michigan State University; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; ML = Macaulay Library, Cornell University; CSA = Constantine and The Sound Approach (2006).
[d]Type E is also referred to as 1A (Summers et al. 2002).
[e]This individual may represent *Loxia scotica* or *L. pytyopsittacus* (Constantine and The Sound Approach 2006).

Acoustic analyses. I analyzed Class I calls with the software Praat version 5.3.04 (Boersma and Weenink 2011). With this program one can measure acoustic variables directly from frequency contours that are algorithmically derived from spectrograms. Using frequency contours removes the need to "eyeball" measurements from spectrograms, which are representations of sounds that can vary do to the amplitude of the signal, analysis window size and shape, etc. (Zollinger et al. 2012). Thus, the process allows for the extraction of accurate, repeatable and unbiased measures. I measured the fundamental frequency, which is the dominant frequency component of Class I calls, with Praat's pitch tracking and extraction tools in the "SoundEditor" window (Fig. 3.2; Chapter 2). I took nine measurements on each call: frequency at start (F1); frequency at end (F2); minimal frequency (F3); maximal frequency (F4); frequency at maximal intensity (F5); mean frequency (F6); duration (D1); maximal intensity (I1); and intensity at maximal frequency (I2).

Statistical analyses. To test for microgeographic trends I used nested analysis of variance (ANOVA) models to estimate variance components attributable to variation among Newfoundland recording sites (n = 10), individuals (n = 83), and calls of individuals (n = 890). Individuals were not banded in this study but crossbill flocks at all sites appeared to consist of single cohesive groups. Therefore I used recording site as a proxy for flock. Variance components were estimated using the linear mixed effects (LME) and varcomp (Paradis et al. 2004) procedures in the statistical program R version 2.14.0 (R Development Core Team 2011). Raw variables did not conform to a normal distribution and were not independent, so I used scores from a principal components analysis (PCA) as dependent variables. Principal components (PCs) with eigenvalues ≥ 1

(Kaiser-Guttman criterion; Jackson 1991) were used in the nested ANOVA models and provided new uncorrelated variables that contained most of the variation in the original dataset.

To further explore variation in the structure of Class I calls of Newfoundland birds, I extracted time-normalized frequency contours. Time normalization was performed by sampling the extracted contours for a fixed number (64) of frequency points at equal time intervals within each call (McCowan 1995). To quantify frequency modulation in Class I calls from Newfoundland birds, frequency change points (FCPs) were quantified by counting the number of directional frequency changes >50 Hz along the call's frequency contour (Fig. 3.2).

I compared Class I calls between Newfoundland, mainland North American and Europe with DA. PCs from a PCA on individual means of calls were used as synthetic uncorrelated variables for the DA (Jombart et al. 2010), using the selection criteria described above. Individual means were used to test whether individuals could be correctly classified to vocal type. To explore effects of data averaging, I also performed a DA on the raw unaveraged data (i.e., at the level of the call).

All data were analyzed using the statistical program R version 2.14.0 (R Development Core Team 2011). See Chapter 2 Methods for further details on field observations, study sites, recording and call characterization protocols.

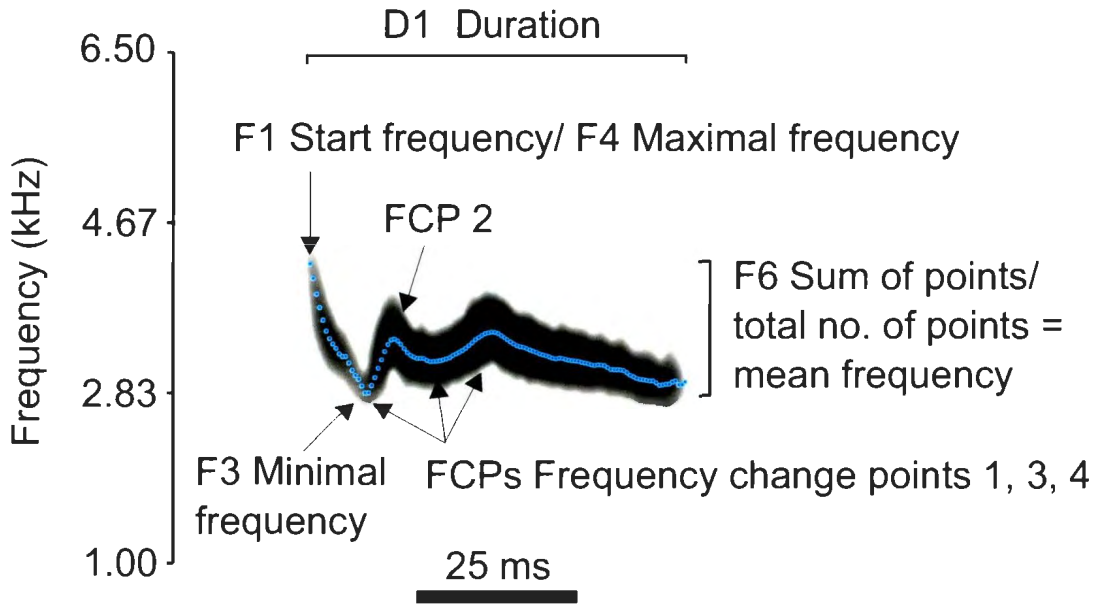

FIGURE 3.2. Examples of acoustic variables used in the study for Class I calls. These were taken from frequency contours (in blue) computed for spectrograms using Praat 5.3.04 (Boersma and Weenink 2011). The interval between successive frequency samples (i.e., spaces between blue points) along the contour was set at 0.0005 s.

3.3 Results

Principal components analyses. PCA for samples summarized in Table 3.2 identified the first four PCs with eigenvalues ≥ 1, accounting for 84% of the variance. Salient variables (i.e., those with loadings > 0.40; Guadagnoli and Velicer 1988) for the first PC were mean frequency (F6), maximal frequency (F4), and frequency at maximal intensity (F5). Salient variables for the second PC were frequency at start (F1), and duration (D1). A PCA using only the individual means for Newfoundland birds produced similar results: the first four PCs produced eigenvalues ≥ 1 and explained 80% of the variance (35, 20, 15 and 10%, respectively). In this PCA, salient variables were mean

frequency (F6) and maximal frequency (F4) for PC1, and intensity at maximal frequency (I2) and maximal intensity (I1) for PC2.

TABLE 3.2. Results of principal components analysis based on individual means of Class I call variables for Red Crossbills (*Loxia curvirostra*; *n* calls = 1135; *n* individuals = 114) recorded on the island of Newfoundland, Canada, mainland North America and Europe (for further details see Table 3.1 in Methods and Appendix Table A.2).

	Variable loadings (Explained variance, Eigenvalue)			
Acoustic variable[a]	PC 1 (36%, 1.8)	PC 2 (20%, 1.3)	PC 3 (17%, 1.3)	PC4 (11%, 1.0)
F6	–0.49	0.03	0.24	–0.18
F4	–0.46	0.26	–0.01	–0.19
F5	–0.43	0.06	0.15	–0.36
F2	–0.39	–0.36	0.08	0.31
I2	–0.27	–0.13	0.60	–0.34
F1	–0.23	0.57	–0.08	0.20
F3	0.23	–0.37	0.36	0.56
I1	0.15	0.29	0.62	–0.01
D1	0.12	0.49	0.19	0.49

[a]F1: Frequency at start; F2: Frequency at end; F3: Minimal frequency; F4: Maximal frequency; F5: Frequency at maximal intensity; F6: Mean frequency; D1: Duration; I1: Maximal intensity; I2: Intensity at maximal frequency.

Nested ANOVAs. Calls from adult Red Crossbills recorded on the island of Newfoundland varied greatly among individuals within recording sites: most variation (71–79%) in nested ANOVAs on the 9 acoustic variables was attributed to among-individual variation (Table 3.3). Variation among calls accounted for the second largest amount (20–27%), and very little variation among sites was revealed (1.6–2.2%).

TABLE 3.3. Individual differences accounted for most variation (71–79%) in Class I calls of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, 4 February to 2 August 2011. Variance components attributable to recording sites, individuals, and within-individual variation are shown using the first four PCs from PCA (see text and Table 3.2). Variance components were estimated using nested linear mixed effects models (calls within adults within recording site).

	Percent of variance among:		
Principal component no.	Recording Site	Individual	Call
1	1.9	73.7	24.3
2	2.2	70.7	27.2
3	2.2	76.1	22.1
4	1.6	78.8	19.6

[1] $P<0.001$, nested ANOVA among recording sites
[2] $P<0.001$, nested ANOVA among individuals within recording sites

Discriminant analyses. DA correctly classified 89% of individuals to the correct vocal type (Fig. 3.3; Table 3.4). A DA based on the unaveraged dataset (i.e., all calls) produced similar results, with 91% of all calls classified to the correct vocal type. Most (98%) of Newfoundland individuals were correctly classified but five of six European individuals were classified as Newfoundland birds. Vocal types from mainland North America were discriminated well by DA, with 86% of individuals classified correctly. Through visual examination of spectrograms, including spectrograms of calls that were misclassified by the DA, I could identify five individuals whose calls were very similar to individuals from mainland North America (Fig. 3.4). A multivariate analysis of variance (MANOVA) showed statistically significant differences among multivariate means for different individuals among vocal groups ($P<0.001$, Wilk's $\lambda = 0.042$). Descriptive statistics on 1135 calls from 114 individuals (~10 calls/individual) assigned to vocal type (North American: 1–4, 6, 7 and 10; Europe: *L. scotica/L. pytyopsittacus*, type E) are shown in Table 3.5.

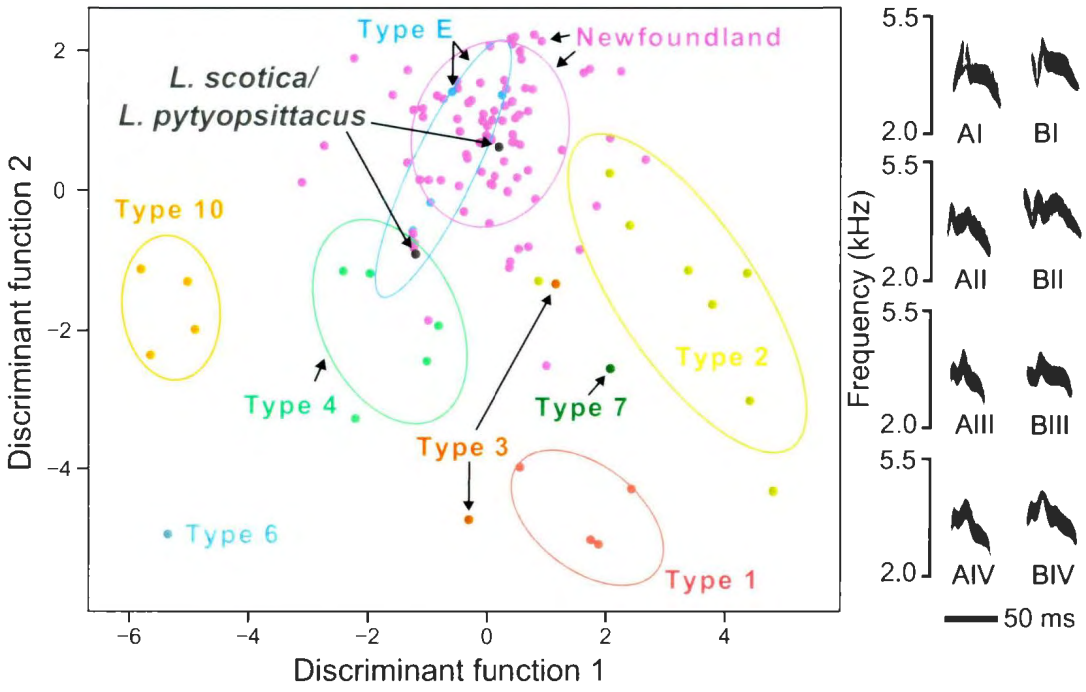

FIGURE 3.3. Class I calls of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland, Canada, differ acoustically from calls recorded elsewhere in mainland North America. This scatterplot shows the first two discriminant functions of a discriminant analysis (DA) on individual means of acoustic variables taken from Red Crossbill Class I calls from mainland North America, Europe and the island of Newfoundland. The DA classified 102/114 (89%) of individuals to the correct vocal type (98% of Newfoundland birds were classified correctly). Vocal types are shown by different colours; dots represent individual birds and ellipses represent 95% confidence intervals for vocal types. Spectrograms show some similarities between flight calls from Newfoundland and European individuals (AI–AIV and BI–BIV, respectively; refer to Appendix Table A.2 for details on samples).

TABLE 3.4. Discriminant analysis correctly classified most Class I calls (n = 1135) of crossbills (*Loxia curvirostra/L. scotica/L. pytyopsittacus*) from mainland North America, Europe, and the island of Newfoundland, Canada (NF). In the first three discriminant functions (DFs), the percentage of between-class variance and corresponding eigenvalues (in parentheses) were: DF1 = 50% (5.4), DF2 = 44% (5.0), DF3 = 5% (1.7).

	Predicted vocal type									
	Mainland North America							Europe		NF
Observed vocal type	T1	T2	T3	T4	T6	T7	T10	E/1A	*L. scotica/L. pytyopsittacus*	NF
T1	3	0	1	0	0	0	0	0	0	0
T2	0	6	0	0	0	0	0	0	0	2
T3	0	0	1	0	0	0	0	0	0	1
T4	0	0	0	5	0	0	0	0	0	0
T6	0	0	0	0	1	0	0	0	0	0
T7	0	0	0	0	0	1	0	0	0	0
T10	0	0	0	0	0	0	4	0	0	0
E/1A	0	0	0	0	0	0	0	0	0	4
L. scotica/L. pytyopsittacus	0	0	0	1	0	0	0	0	0	1
T8	1	0	0	1	0	0	0	0	0	81
% correct assignments	75	75	50	100	100	100	100	0	0	98

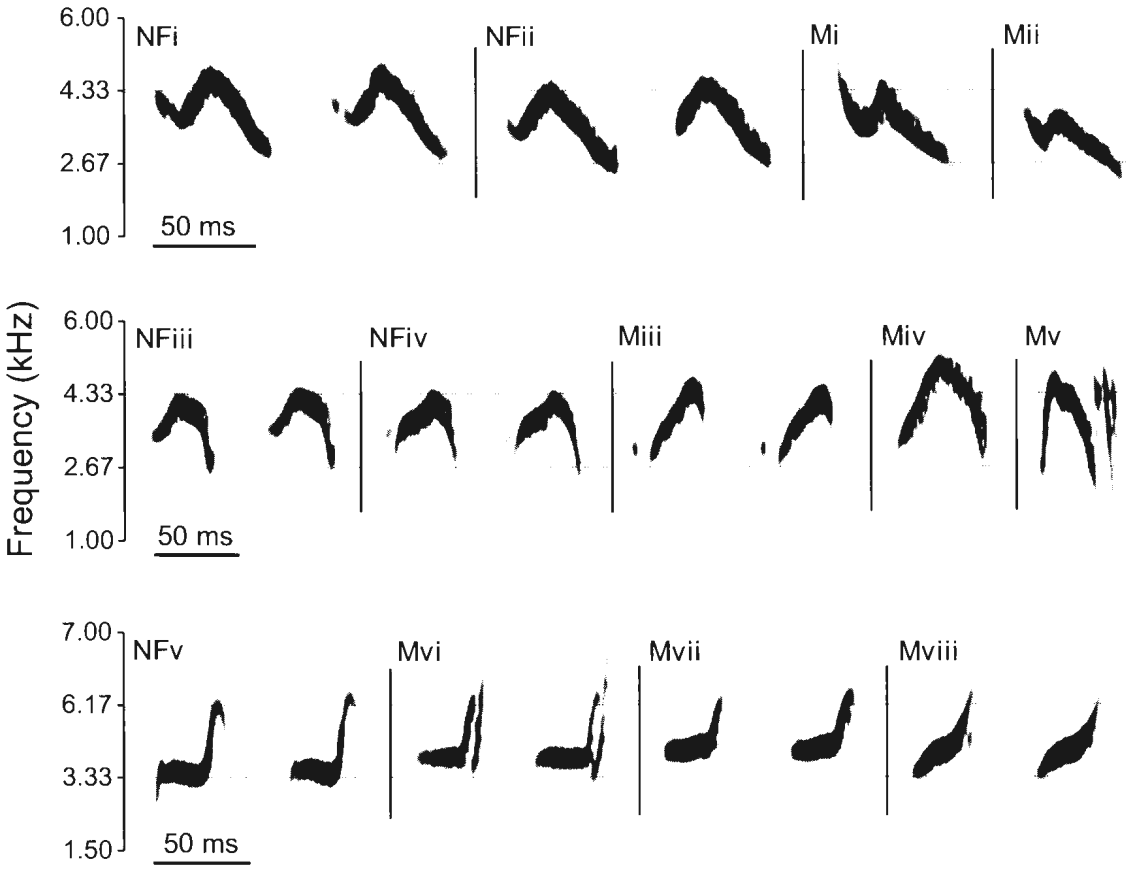

FIGURE 3.4. Multiple kinds of Class I calls of Red Crossbill (*Loxia curvirostra*) were sampled from the island of Newfoundland (individuals NFi–NFv), suggesting the presence of several Red Crossbill forms. Examples of similar calls from other individuals from mainland North American localities (Mi–Mviii) are included for comparison. Vertical bars separate calls from different individuals. Refer to Appendix Table A.2 for details on samples.

TABLE 3.5. Summary of descriptive statistics (means of individual averages ± SD) for frequency (Hz), temporal (ms), and intensity (dB/Hz) variables of Class I calls (n = 1135) from 10 vocal types of crossbill (*Loxia curvirostra* and *L. scotica/L. pytyopsittacus*; n individuals = 114; mean of ~10 calls/individual). [a]F1 = frequency at start of call; F2 = frequency at end of call; F3 = minimal frequency of call; F4 = maximal frequency of call; F5 = frequency at maximal intensity of call; F6 = mean frequency of call; D1 = duration of call; I1 = maximal intensity of call; I2 = and intensity at maximal frequency of call. For details on samples see Table 3.1.

Vocal type (n individuals)	Acoustic variable[a]								
	F1	F2	F3	F4	F5	F6	D1	I1	I2
Island of Newfoundland									
8 (78)	3927 ± 484	3127 ± 534	2901 ± 239	4292 ± 367	3623 ± 180	3525 ± 179	50 ± 6	75 ± 5	59 ± 9
2 (4)	3558 ± 384	2639 ± 454	2606 ± 433	4270 ± 148	3845 ± 65	3665 ± 55	49 ± 1	72 ± 3	66 ± 2
10 (1)	2930	3872	2518	5026	3475	3625	41	76	61
Mainland North America									
1 (5)	4628 ± 935	1843 ± 487	1843 ± 487	5038 ± 822	3998 ± 148	3788 ± 356	45 ± 7	78 ± 9	60 ± 6
2 (7)	4322 ± 485	1837 ± 437	1834 ± 433	4325 ± 484	3461 ± 290	3314 ± 194	51 ± 8	74 ± 6	52 ± 6
3 (2)	4617 ± 513	2404 ± 72	2404 ± 72	5049 ± 282	4000 ± 651	4013 ± 12	54 ± 5	70 ± 7	54 ± 13
4 (5)	4057 ± 1050	4649 ± 863	2434 ± 396	4960 ± 387	3850 ± 120	3723 ± 129	43 ± 6	65 ± 10	46 ± 5
6 (1)	5014	5212	3164	5346	5178	4302	39	57	50
7 (1)	4486	2063	2063	4493	3684	3359	49	61	38
10 (4)	3490 ± 361	5313 ± 166	3418 ± 326	5383 ± 98	4159 ± 138	4112 ± 115	34 ± 1	67 ± 11	51 ± 13
Europe									
E (4)	4051 ± 604	3229 ± 226	3113 ± 176	4483 ± 395	3801 ± 374	3742 ± 198	55 ± 4	70 ± 4	47 ± 4
L. scotica/pytyopsittacus (2)	3762 ± 294	2904 ± 60	2887 ± 50	4408 ± 260	3701 ± 195	3802 ± 30	51 ± 16	69 ± 16	53 ± 7

Most flight calls of Red Crossbills recorded on the island of Newfoundland exhibited rapid frequency modulation (Fig. 3.5). Out of 890 calls, 62% (n = 556) had 4–5 FCPs, producing M-shaped calls (Fig. 3.6; Young et al. 2012). Individuals with calls of fewer or more FCPs often showed variation of a graded nature, e.g., by adding or dropping parts of the beginning or end of calls (Fig. 3.5).

Spectrographic analysis of Class III calls and song. Class III calls from Newfoundland birds were highly stereotyped and varied little among individuals or contexts of use (Chapter 2). Spectrograms from the Newfoundland sample generally differed greatly from mainland North American samples (Fig. 3.1) but resembled calls of Scottish Crossbill (Fig. 3.7).

Newfoundland birds sang a variety of note types and motifs (Chapter 2). Five individuals sang consistent patterns of notes and trills that were distinct from samples from mainland North America (Fig. 3.8).

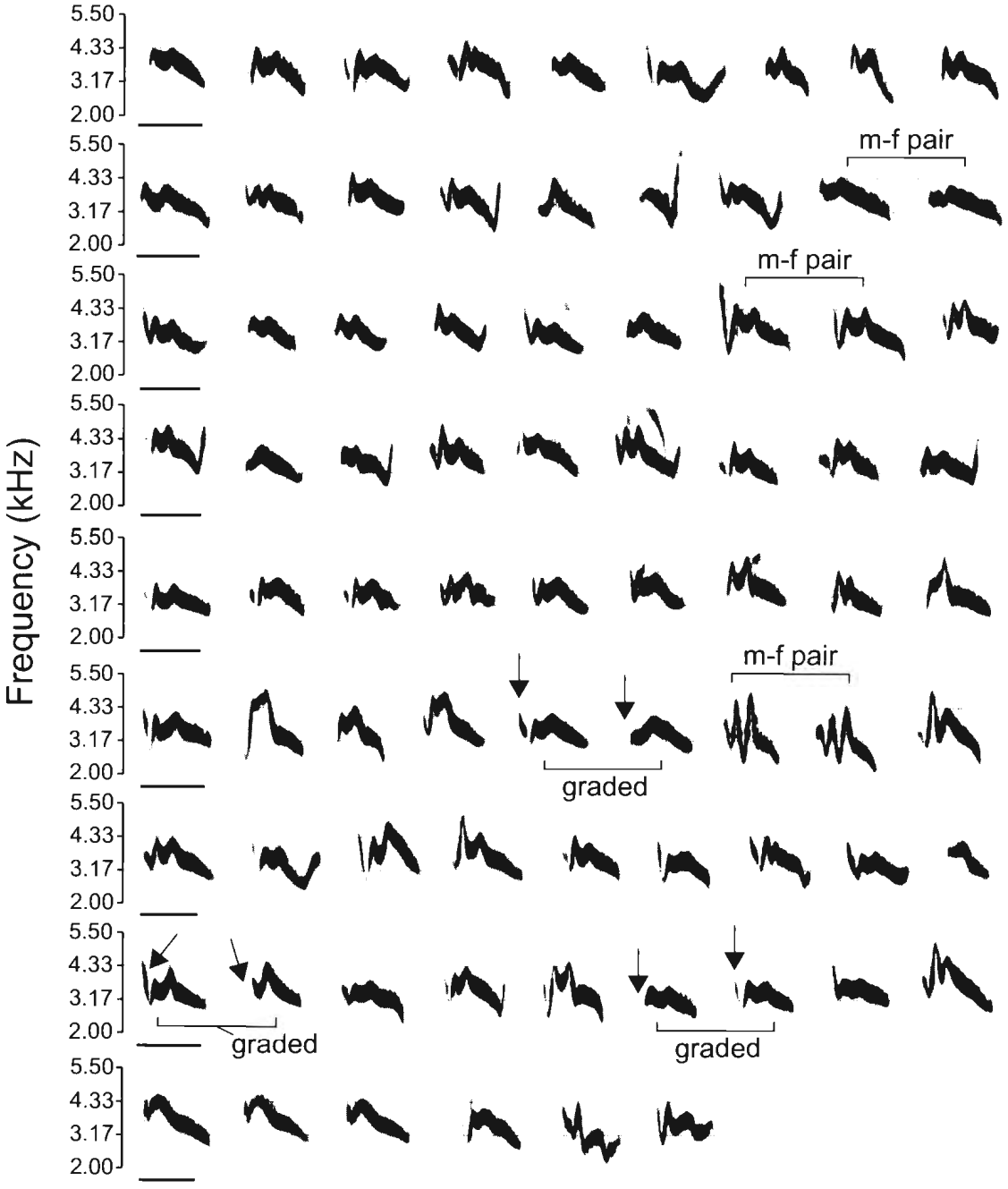

FIGURE 3.5. Class I calls of 78 individual adult Red Crossbills (*Loxia curvirostra*; one spectrogram per individual) recorded on the island of Newfoundland have a common structural plan but vary considerably in frequency modulation. These individuals were acoustically distinct from other vocal types and several of them also emitted a distinctive Class III call (Fig. 3.7; Chapter 2). Hence, these spectrograms may represent calls of *L. c. percna* ("type 8"; Groth 1993). Examples of three presumed pairs are labelled ("m-f pair"), and examples of calls that may represent grading because they differ between individuals only at the beginning or end are marked. Time markers, 50 ms.

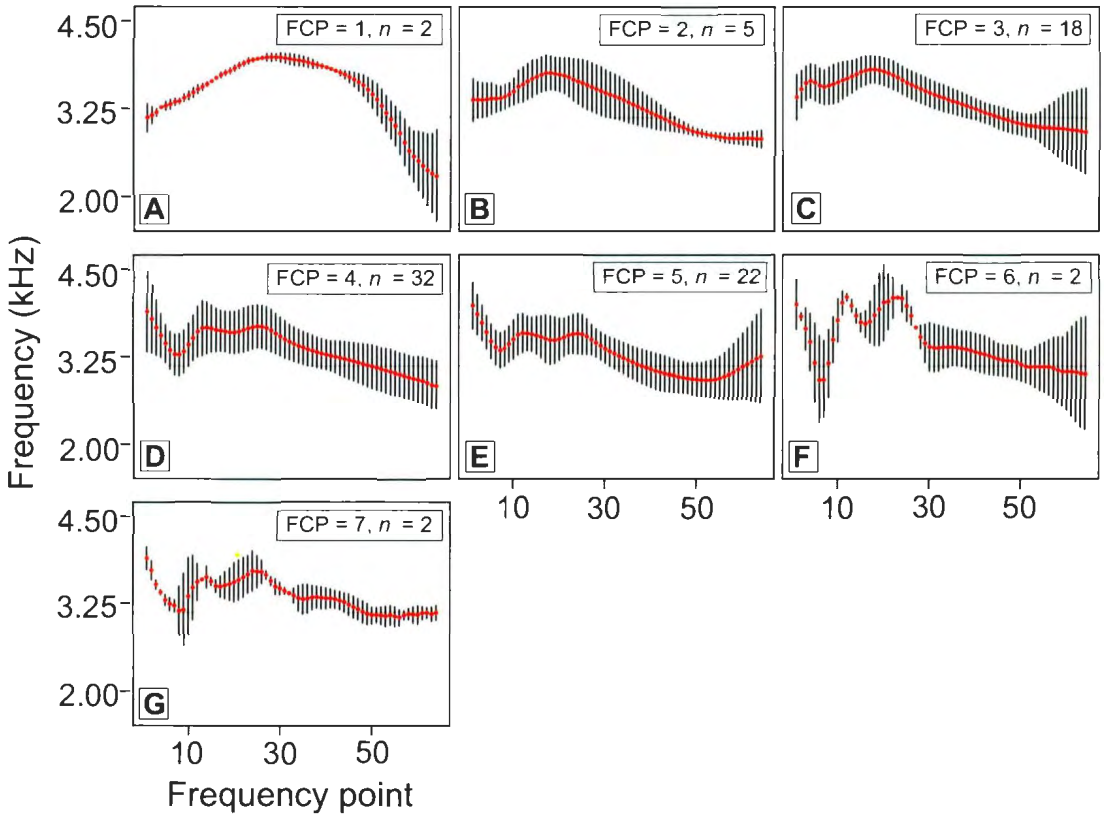

FIGURE 3.6. Frequency modulation occurred in most Class I calls of Red Crossbills (*Loxia curvirostra*) recorded on the island of Newfoundland but varied greatly in expression. This figure shows time-normalized frequency contours that were extracted from 890 Class I calls from 83 individuals. Birds with similar numbers of frequency change points (FCPs; see Methods) were combined; number of adults (*n*) is indicated in each panel. The red lines connect mean frequency point values; black vertical bars represent ± 1 SD.

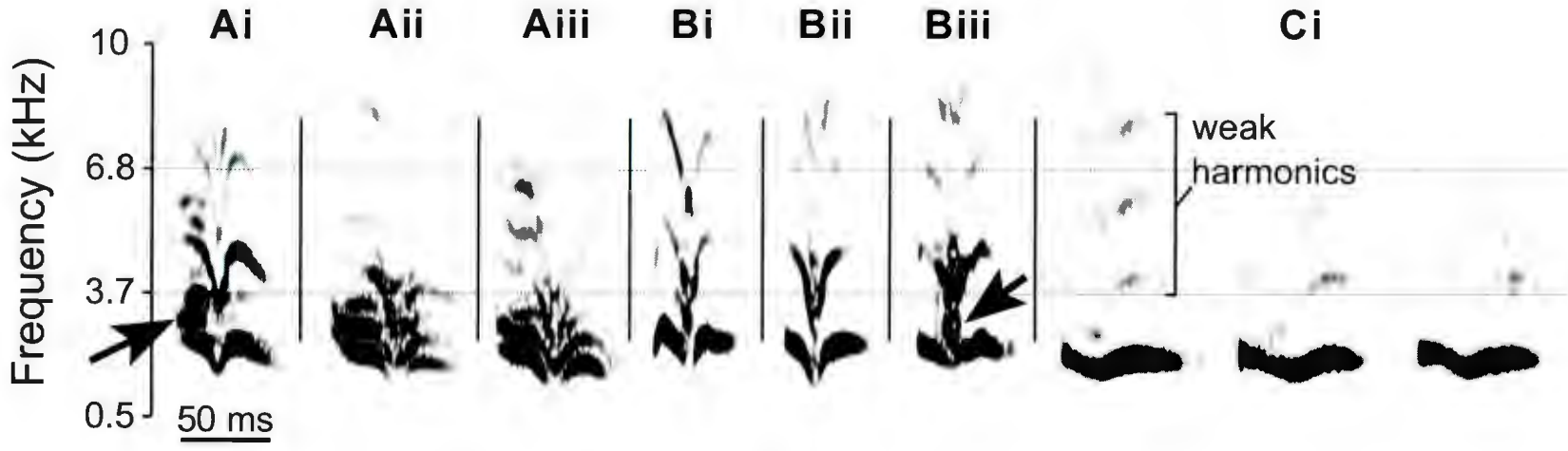

FIGURE 3.7. Spectrograms of Class III calls from three Scottish Crossbills (*Loxia scotica*; Ai–Aiii; individuals separated by vertical bars) shared a similar pattern with Red Crossbills (*L. curvirostra*) recorded on the island of Newfoundland (Bi–Biii). Calls given from an adult male Red Crossbill from Schuyler County, New York, USA (Ci; this individual may represent vocal type 2), are also similar to the Newfoundland samples but show less frequency modulation and weak harmonics. Compared to the Scottish Crossbill samples, calls from Newfoundland birds have less non-linear phenomena (indicated by arrows) and hence do not have the same nasal quality. Details on samples are in Appendix Table A.2.

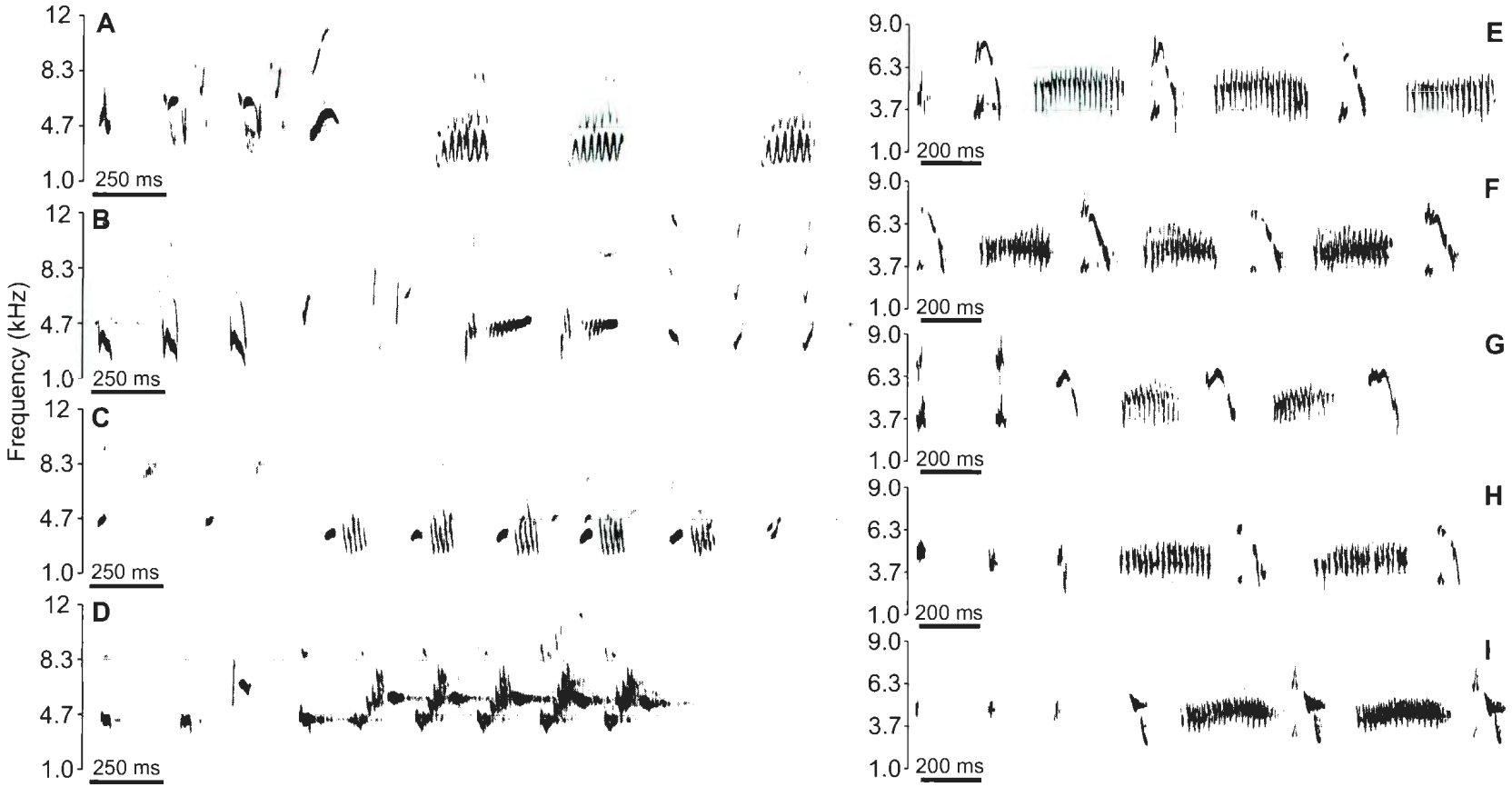

FIGURE 3.8. Song motifs of Red Crossbills (*Loxia curvirostra*) differ between mainland North America (A–D) and the island of Newfoundland (E–I). Details on samples are in Appendix Table A.2.

3.4 Discussion

The unclear systematic position of Red Crossbills on the island of Newfoundland provided the opportunity to test whether vocalizations, found to be informative markers of differentiation elsewhere (Groth 1993a), could resolve the question about whether a distinct vocal form exists on the island of Newfoundland. I analyzed Red Crossbill vocal variation on the island of Newfoundland and compared the findings with samples from elsewhere in North America and Europe.

Crossbills appear to exhibit assortative flocking with shared vocalizations (Smith et al. 2012), therefore variation among flocks (for which I used sites as a proxy) should exceed among-individual variation if sound samples contain more than one vocal type. My analyses disclosed only minor among-site variation. Instead, most acoustic variation was explained by among-individual variation (a common trend in Red Crossbill studies; Groth 1993a), which suggests that a single vocal type dominated Newfoundland samples (but see below). Several individual birds from the island were vocally similar even over hundreds of kilometers. Many of these Class I calls are similar to those that have been recorded from Red Crossbills on Newfoundland dating back to 2005 (Young et al. 2012), but differ from the Class I calls described from an individual bird recorded in Newfoundland in 1981 (Groth 1993a; Appendix: Fig. A.2).

Most individuals were correctly classified by DA, indicating that variation in acoustic variables of Class I calls within vocal types was limited relative to variation between vocal types. The acoustic structure of Class I calls from my Newfoundland sample generally falls within the known range for the species complex, but differ acoustically in some ways from those recorded elsewhere in mainland North America:

most striking is the high degree of frequency modulation exhibited by individuals. Thus, on the basis of both visual examination of spectrograms and audible qualities of calls of the Newfoundland sample, I suggest that most of these individuals (i.e., those shown in Fig 3.5) represent a distinct vocal type from an island form or at least an Atlantic Canada form which may represent *L. c. percna*. Several of these individuals also uttered Class III calls and song motifs that were distinct from those of Red Crossbills from mainland North America (Figs. 3.1 and 3.8). In addition, recent morphological measurements obtained from island birds fall within the known range for *L. c. percna* (Young et al. 2012).

As noted, many Red Crossbills from the Newfoundland sample showed acoustic similarities in Class I calls across study sites on the island, and a DA clustered individuals from the island relatively closely together in relation to samples from other vocal types (Fig. 3.3). However, examination of spectrograms and frequency contour shapes of Class I calls (Fig. 3.5 and 3.6, respectively) revealed overall high variation in frequency modulation among-individuals. A recent study of Red Crossbills vocalizations in the western United States also produced descriptions of Class I calls that included relatively high levels of among-individual spectrographic variation (Irwin 2010). In contrast, descriptions of European (Robb 2000) and other North American mainland vocal types (Groth 1993a) appear to show relatively less among-individual variation in Class I calls. Such apparent differences may reflect: 1) actual inequalities in vocal variability among-individuals across vocal types or, 2) that the range of vocal variation among-individuals within some vocal types may not be, as of yet, adequately described. In addition, acoustic variability within the Call Classes of different vocal types may contribute to apparent among-individual variability within vocal types if workers confuse Call Classes that are

acoustically similar or intergrade (e.g., see similarities between Call Classes I and II; Chapter 2).

My Newfoundland sample also included a small number of Class I calls that are similar to known mainland vocal types (i.e., types 2 and 10; Fig. 3.4), indicating that other North American vocal types also occur on the island of Newfoundland. Several Class I calls from individuals in my Newfoundland sample also resembled mainland forms (i.e., see first three spectrograms in the bottom row of Fig. 3.5), but uttered Class III calls similar to other individuals sampled from Newfoundland (e.g., individuals Bi–Biii, Fig 3.7). This suggests that Class III calls are more diagnostic of birds from the island of Newfoundland.

As noted, my sample of Red Crossbill vocalizations from the island of Newfoundland may represent only a part of a widely distributed form of Red Crossbill in Canada's Maritime region (e.g., Cape Breton Island). Further sampling is badly needed from other areas on the island of Newfoundland (e.g., in the west and southwest), eastern Canada and the Maritime Provinces, and ideally should be coupled with assessments of plumage and morphological characters. Sampling in areas peripheral to the island of Newfoundland could also help determine if the form I describe is an island endemic.

Some Class I and III calls of type E Common Crossbills (from mainland Europe) and Scottish Crossbills strongly resemble some samples from Newfoundland (Figs. 3.3, 3.7). These similarities may represent convergence (e.g., as a by-product of morphological adaptation (e.g., bill size and structure) or as a response to selection pressures wrought by the acoustic properties of their respective habitats [Slabbekoorn and Smith 2002]) because spectrograms from European collections in published sources (e.g.,

Robb 2000, Bergmann et al. 2008, Förschler and Kalko 2009) mainly show differences between European and Newfoundland samples. While some bill measurements (e.g., bill depth) of *L. c. percna* are similar to those of type E Common Crossbills (Groth 1993a, Summers et al. 2002), genetic evidence derived from study skins (P. W. Thomas, in litt. 2012) suggests that Red Crossbills from Newfoundland are differentiable from other European individuals but not from other North American vocal types. These findings are consistent with genetic studies on other North American vocal types (Parchman et al. 2006) and further suggest that similarities in some calls between Newfoundland and European birds are due to convergence and not common ancestry.

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CHAPTER 4. CONCLUSIONS

4.1 General Conclusions and Implications

This study presents the first attempt at a repertoire-wide description of Red Crossbill (*Loxia curvirostra*) vocalizations from the island of Newfoundland. I obtained and analyzed original field recordings of Red Crossbills over 2 ½ years at 10 localities on the island.

Red Crossbills produced six distinct non-song Call Classes. Five Call Classes (i.e., Classes I–III, V and VI) were recorded from adults; two Call Classes were uttered from juveniles (Classes IV and V). Multivariate classifications of Red Crossbill calls, performed on the individual averages of acoustic variables, corresponded closely to Call Classes made on the basis of the social, behavioural, and physical contexts of calling birds, audible qualities of calls, and general appearance of spectrograms.

Call Class II produced the most among-individual variation amongst the three most utilized Classes, i.e., Classes I–III. Class II calls are variable so may have limited use for diagnosing vocal types; vocalizations of this Class appear to represent a graded continuum. Since these calls were only given from groups of birds at close range, individuals may be also relying on other non-vocal communicative cues which could thus reduce the need for discrete, localizable, calls.

Call Classes I and III corresponded with the "flight" and "toops/excitement" calls described by others (e.g., Nethersole-Thompson 1975, Groth 1993). These particular Call Classes contain important taxonomic information as demonstrated by their use in differentiating different *Loxia* forms in both North America and Europe (Groth 1993, Summers et al. 2002, Summers and Jardine 2005); importantly, these Call Classes are

also readily recordable in the field and can be obtained from birds in a non-invasive manner. In the comparative portion of this study, statistical and spectrographic analyses showed that most calls from the Newfoundland sample were distinct from other previously described crossbill forms.

Call Classes I and III were relatively stereotyped among individuals and contexts. Stereotypy in Class III calls might be expected as they are often emitted from crossbills when avian predators are near; misinterpretation of such calls could have deleterious consequences (Breed and Moore 2011). Acoustic characteristics of calls from Class I were also generally conserved among individual crossbills and across contexts of use. These "M-shaped" calls vary considerably in frequency modulation but have a common structural plan; they have been recorded in Newfoundland as far back as 2005 (Young et al. 2012). Several Red Crossbills from the island of Newfoundland also uttered distinct stereotyped song elements, further indicating that these individuals represent a distinct vocal form.

This study will serve as a baseline for future work on the island that aims to link diagnostic calls with bill measurements. Such work would help reinforce my findings, i.e., a distinct form of Red Crossbill (possibly *L. c. percna*) exists on the island of Newfoundland. Future work that occurs elsewhere in Atlantic Canada (e.g., Cape Breton Island) may help determine whether this form occurs more extensively across Canada's Atlantic Provinces, or if it is endemic to the island of Newfoundland. In addition, I showed that other vocal types of Red Crossbill occur on the island. Thus, future work involving Red Crossbill population monitoring in Newfoundland should, as a minimum,

include the collection and analysis of acoustic data as an aid to differentiate amongst these cryptic forms.

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APPENDIX

TABLE A.1. Call Class 1 calls do not differ acoustically between adult Red Crossbills in flight or perched. Only one of 14 individuals recorded in both contexts expressed differences (bird #3, for variables F3, F5 and F6, by paired Wilcoxon test). Data shown are means computed on samples (*n*) ranging from samples of 2-10 Class I calls recorded per individual.

Individual		*n*	F1	F2	F3	F4	F5	F6	F7	F8	I2	D1
1	flight	4	3186	3251	2901	3842	3512	3382	43704	941	73	0.047
	perched	4	3392	3086	3032	4059	3695	3545	40785	1027	74	0.049
	z		-1.83	1.10	-1.83	-1.46	-1.83	-1.83	1.46	-1.10	0.00	-1.67
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
2	flight	7	3347	2574	2574	4926	3879	3650	115080	2352	67	0.050
	perched	7	3140	2433	2433	4732	3688	3452	112824	2299	66	0.048
	z		-1.35	-1.18	-2.20	-1.18	-1.52	-1.86	0.00	-0.34	-1.35	-0.85
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
3	flight	10	4097	2946	2422	4132	2801	3086	90255	1711	57	0.056
	perched	10	4140	3074	2726	4245	3140	3315	104493	1519	56	0.048
	z		0.56	2.09	1.07	2.80	2.80	2.80	2.19	-1.89	-0.56	-2.80
	p		*ns*	*ns*	**0.002**	*ns*	**0.002**	**0.002**	*ns*	*ns*	*ns*	*ns*
4	flight	7	4274	3089	3089	4274	3722	3555	61742	1185	57	0.048
	perched	7	4609	3161	3140	4609	3784	3613	70999	1469	53	0.051
	z		1.69	-0.51	1.01	1.86	1.01	1.52	1.18	1.69	-1.35	1.44
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
5	flight	3	3258	3073	3073	3698	3485	3446	46638	625	66	0.040
	perched	3	3391	3343	3333	3882	3817	3615	50988	550	65	0.042
	z		-1.60	-1.60	-1.60	-1.60	-1.60	-1.60	-1.07	0.00	0.00	-1.07
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
6	flight	5	5090	2628	2628	5090	3638	3586	92517	2461	44	0.065
	perched	5	5189	2598	2598	5189	3846	3638	100945	2592	49	0.063
	z		-0.40	0.13	-0.40	0.13	-2.02	-1.75	-2.02	-0.13	-2.02	1.21
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
7	flight	3	3803	2780	2780	4335	3741	3673	64420	1555	69	0.059

	perched	3	4074	2881	2841	4535	3860	3799	61591	1694	66	0.059
	z		1.07	1.60	1.60	1.07	0.53	1.60	0.00	1.07	-0.53	0.53
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
8	flight	5	3570	2760	2740	4202	3838	3554	55467	1462	72	0.057
	perched	5	4065	3017	2875	4479	4020	3779	60967	1604	66	0.060
	z		2.02	2.02	2.02	1.75	1.48	2.02	1.48	1.21	-1.48	1.21
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
9	flight	3	2891	2291	2291	4107	3786	3610	78864	1816	65	0.047
	perched	3	3417	2032	2032	4133	4084	3547	88170	2101	69	0.051
	z		1.60	-1.60	1.07	-1.60	1.60	-1.07	1.60	1.60	1.07	1.39
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
10	flight	8	2891	2291	2291	4107	3786	3610	78864	1816	65	0.047
	perched	8	3417	2032	2032	4133	4084	3547	88170	2101	69	0.051
	z		1.82	2.10	2.52	2.10	1.68	2.38	0.84	1.54	0.42	-1.62
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
11	flight	8	4195	3148	2937	4195	3221	3302	57065	1258	52	0.055
	perched	8	4231	3159	2953	4231	3377	3293	50172	1278	57	0.056
	z		0.42	0.28	0.42	0.98	0.98	0.56	-1.26	0.42	2.10	1.26
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
12	flight	2	4433	2818	2818	4433	3436	3295	52776	1615	57	0.068
	perched	2	4589	2982	2982	4589	3698	3454	49466	1607	58	0.064
	z		0.45	1.34	0.45	1.34	1.34	1.34	-1.34	-0.45	0.45	-1.34
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
13	flight	2	4003	2986	2973	4514	3924	3762	79399	1541	75	0.050
	perched	2	3767	3010	3010	4456	3762	3692	68462	1446	65	0.054
	z		-0.45	1.34	-0.45	1.34	-1.34	-1.34	-1.34	-1.34	-1.34	0.45
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
14	flight	9	4078	3104	3067	4220	3638	3576	65437	1153	63	0.054
	perched	9	3900	3184	3153	4449	3740	3677	77472	1296	70	0.052
	z		-1.72	1.60	2.67	2.19	2.31	2.55	2.43	1.84	-1.95	-1.54
	p		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*

NOTE: P-values are given for paired Wilcoxon tests. Values in boldface type indicate statistical significance after a Bonferroni correction ($\alpha' = \alpha/13 = 0.0038$). See Methods for descriptions of variables.

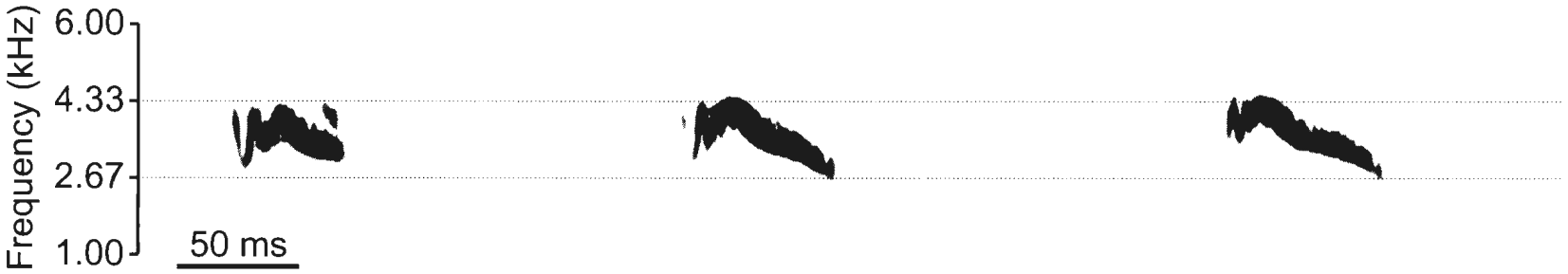

FIGURE A.1. This Red Crossbill (*Loxia curvirostra*) individual alters the shape of its calls during a bout (spectrogram depicts a natural vocal sequence). Recorded in Clarenville, Newfoundland, Canada, on 27 June 2011.

TABLE A.2. Locations, dates and sources of recordings for used for spectrograms featured in Figures 3.3, 3.4, 3.7 and 3.8.

Individual	Vocal type	Location (coordinates)	Date	Source [a]	Notes
AI	type 8 candidate	Whitbourne, NL (47°24' N, 53°31' W)	1 Jult 2012	This study	Immature ♂, yellow orange plumage, faint streaking visible on breast
AII	type 8 candidate	Conception Bay South, NL (47°30' N, 52°55' W)	17 June 2011		Adult
AIII	type 8 candidate	Conception Bay South, NL (47°30' N, 52°55' W)	17 June 2011		Adult
AIV	type 8 candidate	South River, NL (47°30' N, 53°17' W)	1 June 2011		Adult
BI	E	Netherlands: De Kennemerduinen, Bloemendaal, Noord-Holland	14 March 1998	Robb 2000: Track 40	
BII	E	Netherlands: De Kennemerduinen, Bloemendaal, Noord-Holland	21 February 1998	Robb 2000: Track 40	
BIII	E	Netherlands: De Hoge Veluwe NP, Apeldoorm/Arehem/Ede	13 February 1999	Robb 2000: Track 40	
BIV	?[b]	Scotland: Glencat, Aberdeenshire	25 April 1983	Robb 2000: Track 49	
NFi	2	Upper Gullies, NL (47°29' N, 53°02' W)	6 June 2011	This study	Adult ♂
NFii	2	Upper Gullies, NL (47°29' N, 53°02' W)	6 June 2011		Adult ♀, probably mate of NFi
NFiii	2	Clarenville, NL (48°10' N, 53°58' W)	27 June 2011		Adult, sex unknown
NFiv	2	Clarenville, NL (48°10' N, 53°57' W)	26 June 2011		Adult, sex unknown
NFv	10	Clarenville, NL	18		Adult (adult male-female pair

		(48°10' N, 53°57' W)	February 2011		present)
Mi	2	California, Carmen Valley (39° 43' N, 120° 28' W)	11 June 1994	ML 106639	Adult ♂
Mii	2	California, Carmen Valley (39° 43' N, 120° 28' W)	11 June 1994	ML 106639	Adult ♂
Miii	2	Michigan, Luce County	15 July 1987	MVZ 4659	Juvenile
Miv	2	California, Alameda County	25 October 1986	MVZ 5349	Adult ♀
Mv	2	Virginia, Montgomery County	20 March 1984	MVZ 2554	Adult ♂
Mvi	10	Michigan, Chippewa County (46° 24' N, 84° 59' W)	9 April 2011	AV 12830	Adult
Mvii	10	Michigan, Chippewa County (46° 24' N, 84° 59' W)	9 April 2011	AV 12830	Adult
Mviii	10	Maine, Washington County (44° 51' N, 67° 11' W)	16 July 1998	ML 112167	Adult ♂
Ai	*Loxia scotica*	Loch Baa, Highland, Scotland	24 February 1999	Robb 2000: Track 50	
Aii	*Loxia scotica*	Loch Baa, Highland, Scotland	24 February 1999	Robb 2000: Track 50	
Aiii	*Loxia scotica*	Ardgay, Highland, Scotland	20 March 2002	CSA: Track 87	Adults at nest
Bi	type 8 candidate	Howley, NL (49°10' N, 57°05' W)	2 May 2011	This study	Adult ♂
Bii	type 8 candidate	Goulds, NL (47°27' N, 52°44' W)	1 August 2011	↓	Adult ♂
Biii	type 8	South River, NL	1 June 2011	↓	Adult

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	candidate	(47°30' N, 53°17' W)			
Ci	unknown	New York, Schuyler County	16 May 1998	ML 113520	Adult ♂
A	unknown	California, Carmen Valley (39° 43' N, 120° 28' W)	11 June 1994	ML 106640	Adult ♂
B	2	California, Marin County	30 March 1998	ML 111009	
C	10	New York, Tompkins County	17 May 1998	ML 130478	
D	1	New York, Madison County (42° 46' N, 75° 47' W)	5 August 2006	ML 137498	
E	type 8 candidate	Conception Bay South (47°30' N, 52°55' W)	4 February 2010	This study	Adult ♂
F	type 8 candidate	La Manche (47°10' N, 52°55' W)	7 July 2011		Adult ♂
G	type 8 candidate	Howley (49°10' N, 57°05' W)	1 June 2010		Adult ♂
H	type 8 candidate	South River (47°30' N, 53°17' W)	8 June 2011		Adult ♂
I	type 8 candidate	Upper Gullies (47°29' N, 53°02' W)	21 June 2011		Adult ♂

[a]AV = Avian Vocalizations Center, Michigan State University; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; ML = Macaulay Library, Cornell University; CSA = Constantine and The Sound Approach 2006.

[b] This individual may represent *Loxia scotica* or *L. pytyopsittacus* (Constantine and The Sound Approach 2006)

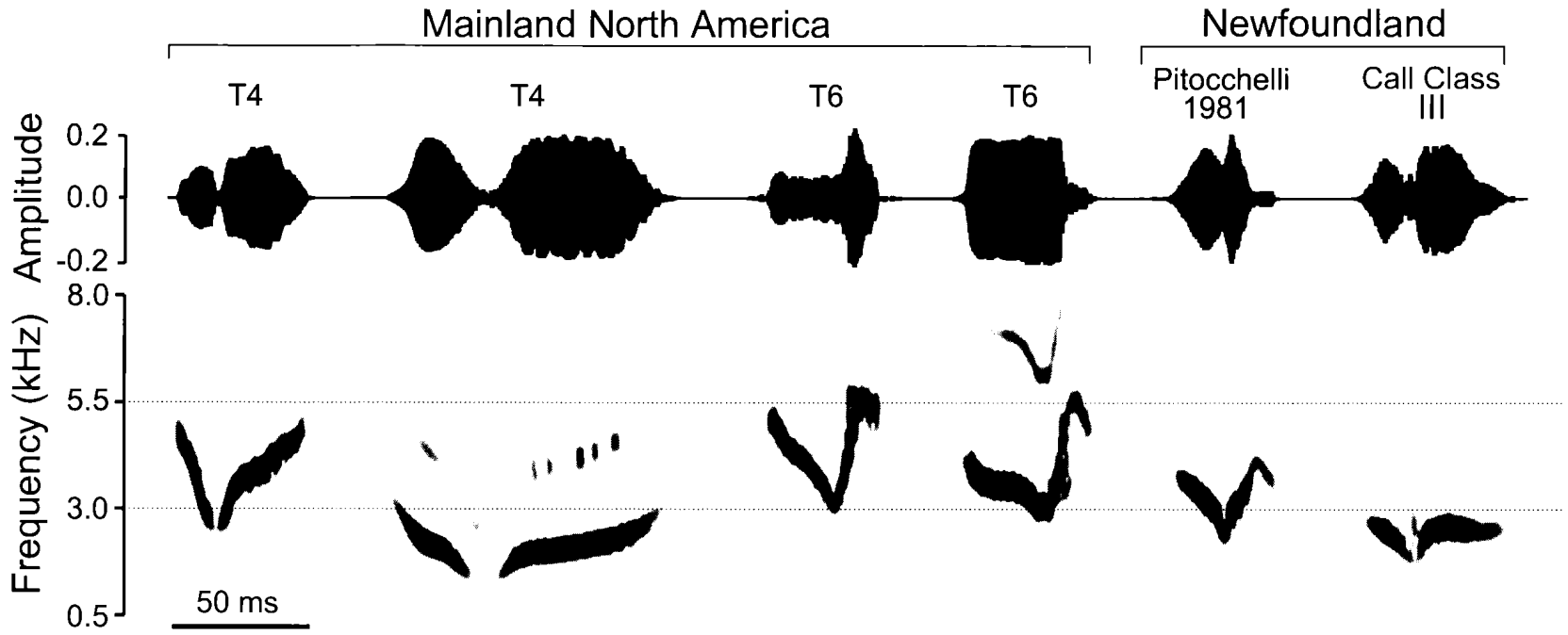

FIGURE A.2. Spectrograms and waveforms of Class I calls from North American Red Crossbill (*Loxia curvirostra*) vocal types (shown under T4 and T6; vocal types 4 and 6, respectively) resemble Class III calls from Newfoundland birds and Class I calls recorded by Pitocchelli in 1981 (see Groth 1993). Pitocchelli's calls are intermediate between Class III calls and some type 6 Class I calls; Groth categorized calls recorded by Pitocchelli as "type 8" Class I calls.